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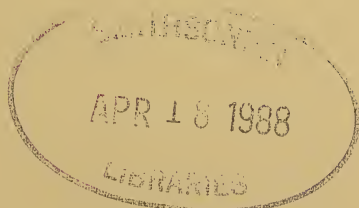
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Frontispiece. Subadult Bolson tortoise (*Gopherus flavomarginatus*), approximately 250 mm plastron length, emerging from a thicket of Candelilla (*Euphorbia antisiphilitica*) at the MAB Reserva de Mapimi, Durango, Mexico. Photograph by Dr. Michael A. Recht.



THE ECOGEOGRAPHY OF THE MEXICAN BOLSON
TORTOISE (*GOPHERUS FLAVOMARGINATUS*):
DERIVATION OF ITS ENDANGERED
STATUS AND RECOMMENDATIONS
FOR ITS CONSERVATION

edited by

DAVID J. MORAFKA¹

C. J. MCCOY

Curator, Section of Amphibians and Reptiles

ABSTRACT

This study defines Bolson tortoise distribution both geographically and ecologically. It proceeds to derive current distribution in the context of historical biogeography, and concludes with prognosis for future viability of the species. Former estimates of the distribution for *Gopherus flavomarginatus* enscribe the entire 50,000 km² of the Bolsons de Mapimi of Chihuahua, Durango, and Coahuila. Our data indicate that the surface areas actually occupied are smaller by an order of magnitude, and highly disjunct.

Detailed topographical analyses of the Mapimi bolsons indicate that only approximately 6000 km² of the area sustain tortoise populations, or are ecologically continuous and geographically contiguous with areas that sustain populations. We estimate a population of not more than 10,000 adults for the entire species (extrapolated from local colony density data).

Analysis of factors coincidental with tortoise distribution identifies three important variables: human induced extirpation—42%, relief—36%, and playsas—22%. These elements set peripheral limits for tortoise distribution and fragment local populations into six major districts.

Microdistributional factors also contribute to the distributional patchiness. In particular, the occasional organization of tortoise populations into tightly packed nuclear areas, possibly social colonies, contributes to uneven distribution within continuous belts of suitable habitat. With 33 environmental variables, we categorized localities in terms of paired variables (tortoise density and an ecological factor) and by their collective similarities (all variables combined). Only human extirpation and soil calcium produced significant correlations with tortoise density. When all environmental variables were considered in "between site" comparisons, localities clustered together only on the basis of geography or slope. One extralimital site, representing *Gopherus agassizii* habitat, was distinctive from all the rest, largely due to gravel substrate and reduced grasses.

Several historical factors may govern extant tortoise distribution. The fossil record indicates that *Gopherus* ranged from Kansas south to Aguascalientes, Mexico, and from Arizona to Florida at various times during the Pliocene and Pleistocene. Distribution may have been maximal in the Pliocene (Blancan). Range may have decreased by 30–50% when late Pliocene–early Pleistocene uplifts extirpated the species from the south central Mexican Plateau (Saladan Subprovince—Aguascalientes). Increased continentality of post-glacial climates, concomitant deterioration of grassland, and disruptions by regional uplifts and glaciopluvial lakes are all seen as molding modern tortoise distribution. Also, members of this genus share major physical and ecological characteristics with the Pleistocene megafauna subject to mass extinction at the end of Pleistocene times. The relatively recent reduction in tortoise range and maximum body size correlate both temporally and spatially with increasing human extirpation. No comparable correlations have been established for ecological factors, either present or past. These findings argue strongly for the validity of Martin's Pleistocene overkill hypothesis in explaining the current limited distribution of this large-sized tortoise. The Bolson tortoise is now endangered with extinction due to habitat loss and human depredation. Current conservation measures are sufficient only to ensure protection of a few populations in Mapimi and Diablo districts. Those

¹ Department of Biology, California State University, Dominguez Hills, Carson, CA 90747.
Submitted 27 April 1987

at the western and northeastern periphery of the species' range may well be extirpated before the end of this century.

INTRODUCTION

This investigation quantifies habitat characteristics of the Bolson tortoise (*Gopherus flavomarginatus*) and the topographic and geographical conditions coincidental with distributional limits of the species. We derive the current ecological circumstances of the tortoise not only in terms of existing conditions, but also from its phylogenetic and paleoecologic history. We statistically determine the frequency, extremes, and correlations for standard sets of ecological variables measured at study sites where the species now occurs. Comparisons are made between these sites and contiguous sites now extralimital to the species, including settings of suspected extirpation. Since the full set of sites is not random, systematic, or normally distributed relative to tortoise presence or absence, our analyses are more descriptive than discriminatory. Even so, quantification of ecological conditions and patterns should provide an improved basis for understanding *G. flavomarginatus* ecology and biogeography. Likewise, our historical analysis of current conditions may elucidate long-term temporal patterns and causal agents that would not otherwise be evident.

Gopherus flavomarginatus is still a new animal to biology. During the 27 years that have passed since the original description (Legler, 1959), literature regarding this species has been largely descriptive and anecdotal, concerned primarily with defining its morphology, general habits and extant distribution (Legler and Webb, 1961; Pawley, 1975; Auffenberg and Franz, 1978; Smith and Smith, 1979; Morafka et al., 1981; Morafka, 1982). The only quantitative analyses of the species are studies of home range and movements (Aguirre et al., 1984) and normal hematology (Morafka et al., 1986). The primary basis of this analysis is distributional information, collected from three sources: museum records, prior literature, and, most particularly, our field surveys. Morafka (1977, 1982) mapped specimens in major United States museum collections. Fossil tortoise distributional information was drawn from Strain (1966), Auffenberg (1974), Brattstrom (1961), Moodie and Van Devender (1979), Van Devender et al. (1976, 1987), Bramble (1982), and Messing (1986).

This organism is the largest living land reptile in North America outside the tropics, and it is probably a key organism to the community organization of the Mapimian grasslands of the Chihuahuan Desert. These desert bunch grass/shrub complexes more closely resemble, at least at the generic level, the biotic assemblages of Tertiary North America's pre-desert "Mojavia" (Axelrod, 1958; Morafka, 1978; Van Devender, 1986) than any other existing refugium. Resemblance is expressed not only in differentiation and phylogenetic position of represented taxa, but probably in community structure as well. High species density and lack of segregation into discrete communities characterized by a single dominant are two such conditions, both more reflective of Tertiary and/or subtropical conditions than most other North American desert ecosystems. Increased knowledge of the *G. flavomarginatus* niche in this ecosystem should not only yield insights into paleoecology of preglacial North America, but also into the events which reduced large vertebrate diversity in the millennia immediately following the last glacial. This tortoise shares many characteristics with the extinct megafauna which so suddenly disappeared from the North American continent. As a survivor of some unknown extinction event that culled many organisms from the same general

guild, the Bolson tortoise becomes particularly important in terms of its natural history and vulnerability to both natural and induced catastrophe.

Institutional abbreviations used in this manuscript are as follows:

KU = University of Kansas

MSUM = Michigan State University

UIMNH = University of Illinois

USNM = National Museum of Natural History

UU = University of Utah

ACKNOWLEDGMENTS

This reports draws upon more than a decade of data. Data gathering has been funded by both private and public agencies, and assisted by a large number of individuals. Field surveying in 1973, 1974, 1975, 1979–87 (1986 WWF ref. #3109) has been possible only because of repeated and generous funding by the World Wildlife Fund. World Wildlife Fund administrators have been exceptionally patient, understanding, and supportive. We would particularly like to thank Curt Freeze, Nancy Hammond, and Tom Lovejoy. Demographic studies have been subsidized by the U.S. Office of Endangered Species (1980–82), and the U.S. Fish and Wildlife Service. Drs. C. Kenneth Dodd, Jr., Clyde Jones, Norman J. Scott, Jr., and Thomas H. Fritts were U.S. agency scientists who made invaluable contributions to this study. Dr. Fritts undertook an extensive series of field interviews, translations, and site inspections on our behalf in 1982. The National Science Foundation International Program sponsored our investigations in collaboration with Mexico's Consejo Nacional de Ciencia y Tecnologia (CONACYT) in 1980–81 (NSF INT. 80-04351), and 1985–86 (NSF INT. 85-04154), thereby providing substantial support for our field efforts. We particularly thank NSF Latin American Program officer Christine E. French for facilitating the coordination of U.S. and Mexican proposals, sometimes under extremely difficult circumstances.

Equally critical support was awarded by the U.S. Fish and Wildlife Service (Contract #14-16-009-81-060) and the USA–Mexico Joint Committee on Wildlife Conservation (Subproject A-1.82, funded by U.S. Fish and Wildlife Service, Region 2—Albuquerque). The following U.S. Fish and Wildlife Service personnel assisted R. B. Bury in field surveys and photodocumentation: H. H. Welsh, J. A. Whelan, W. S. Lippincott, and D. E. Biggins. J. A. Whelan also executed Figures 2 and 3. Most other figures are the work of D. Hadley, Photosphere Studios, Santa Monica, California.

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Mexico's Instituto de Ecologia provided matching funds and personnel which proved indispensable to the success of this investigation. We are particularly grateful to our Mexican collaborator, M. en C. Gustavo Aguirre Leon, and for the financial support awarded by his government (Secretaria de Educacion Publica, Consejo Nacional de Ciencia y Tecnologia, Project #ICECXEU-000483). We are also appreciative of the support of former and present institute directors, Drs. Gonzalo Halffter and Pedro Reyes Castillo.

We are indebted to several of our U.S. colleagues, especially for the use of population density maps. Major contributions were made by Drs. Gary Adest and Michael Recht, and the dozen students and volunteers working under their supervision in the summers of 1980–82. Ing. Jose Treviño and Pablo Dominguez of Mexico's national wildlife service, a division of the Secretaria de Desarrollo Urbano y Ecologia, generously granted permission to use maps and data collected on their field surveys. Ariel Appleton of the Audubon Research Ranch shared many insights with us about the potential impact of overgrazing on the behavior, ecology, and viability of Bolson tortoises, several of which inspired aspects of this study. We thank Margaret Canon for her swift and accurate preparation of the final manuscript. Finally, we wish to thank the Mexican national wildlife service for permits authorizing field work on the Bolson tortoise. Shells, salvaged as voucher material, were imported under a U.S. Fish and Wildlife permit to R. B. Bury in 1982–83. These samples have been deposited in the National Museum of Natural History, Washington, D.C. Additional voucher material has been deposited in The Carnegie Museum of Natural History.

PART I. DISTRIBUTION, ABUNDANCE AND STATUS OF THE BOLSON TORTOISE

R. BRUCE BURY¹

DAVID J. MORAFKA

C. J. MCCOY

INTRODUCTION

The Bolson tortoise (*Gopherus flavomarginatus*) is relatively new to science, having been formally described less than 30 years ago (Legler, 1959). Undoubtedly it escaped recognition until recently partly due to the isolated range of the species in remote, enclosed basins of the Chihuahuan Desert in north-central Mexico. Although this region is only 150–300 km south of the United States border, it is so poorly known that there are continuing controversies about topographic and place names as well as regional boundaries. The desert and steep mountain terrain of the area have limited human occupation.

The tortoise likely once occurred in an area now divided by Mexican Highway 49, a major north–south paved highway, from Escalon, Chihuahua, and southward to Ceballos and Banderas, Durango (Fig. 1). Lands surrounding these towns in northern Mexico were converted to farmland in the 1920s, and tortoises probably disappeared in these areas by the 1930s.

Assessment of the distribution and status of populations is increasingly important because the Bolson tortoise is a large herbivore in the Chihuahuan Desert and, because of its scarcity, it is now on the U.S. Endangered Species List. Prior accounts of the species (Legler, 1959; Legler and Webb, 1961; Morafka, 1982) present only general approximations of distributional limits and little field survey data. Here, we provide a detailed account of the tortoise's distribution, assess its abundance at several 25–50-ha study sites, and examine aspects of its population biology.

METHODS

Since 1970, we have collectively spent over one calendar year (equivalent to about three person years) in field research on the species. Most field surveys were undertaken in July 1980, July–August 1981, and March–April 1982. We visited every previously known locality for the Bolson tortoise and many new areas. During field surveys, four to eight investigators walked 5–10 m apart across favorable habitat, searching for any tortoise sign. We purposely avoided upland rocky slopes and open, barren lagunas (dry lake beds) because these habitats do not harbor tortoises. Some sites were randomly selected by simply stopping along dirt roads and heading out across the bolsons. These bolsons are flat or gently rolling desert valleys surrounded by mountains and draining into shallow lagunas (ancient lake beds) in the center.

When at ejidos (cooperative farms) or ranches away from towns and cities, we interviewed people at every opportunity. We asked if they knew of any tortoises in the area, if they could distinguish

¹ National Ecology Research Center, U.S. Fish and Wildlife Service, 1300 Blue Spruce Drive, Fort Collins, CO 80524.

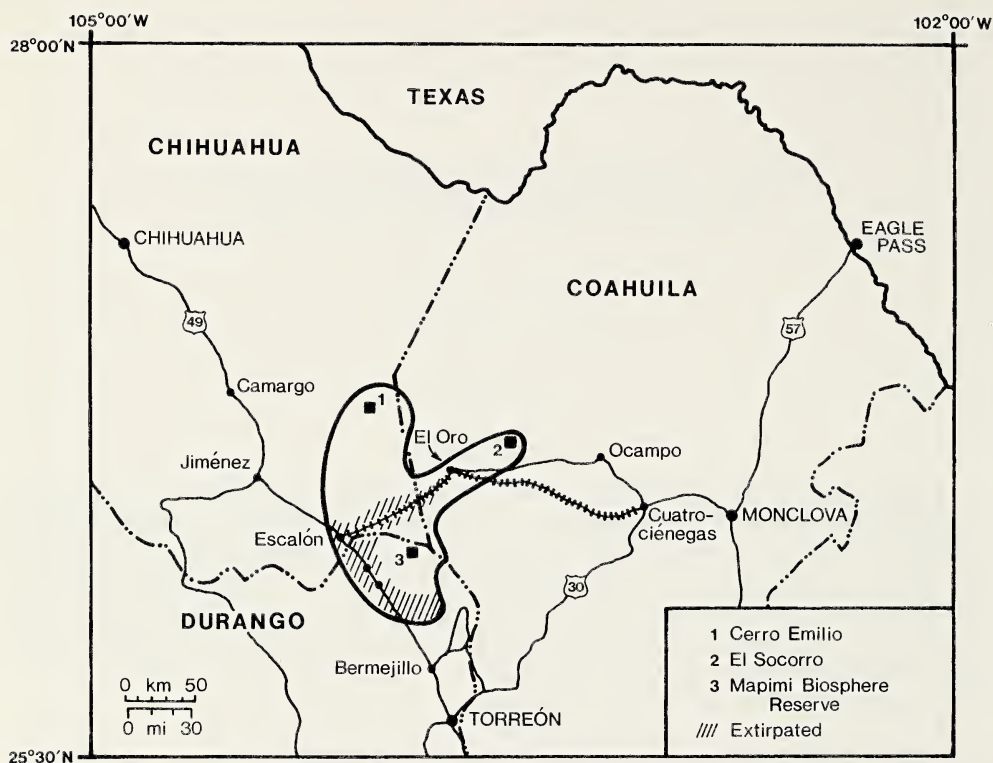


Fig. 1.—General map of the distribution of *Gopherus flavomarginatus*.

tortoises from other turtles (because mud turtles occur in the region), their length of residency or familiarity with the area, and any natural history they would like to relate to us. We told residents that we were biologists interested only in learning about tortoises. Generally, we were in the U.S. Government vehicles with decals indicating our affiliation. Whenever residents suggested that tortoises might occur in an area, we attempted to search these sites first because the reports were usually true.

We employed a quadrat and grid location technique (Bury and Luckenbach, 1977) to collect data on tortoise populations at two 25-ha plots. A similar system was used on a 76-ha plot by Aguirre et al. (1984). However, this technique was designed to census the Desert tortoise (*Gopherus agassizii*), a species that usually can be intercepted outside of its burrow. The Bolson tortoise is much more secretive than the Desert tortoise. For example, G. Adest (personal communication) measured only episodic surface activity (10–40 min/day) in the Bolson tortoise, during the annual nine-month Chihuahuan Desert dry season. We did field surveys and study plots primarily during the dry season because access to remote locations is difficult in the July-to-September rainy season. As a result, most of our results are based on tortoise sign (burrows, scats, or shells; Table 1).

Aguirre et al. (1984) reported that Bolson tortoises shared burrows and used more than one burrow per year at the MAB Mapimi Reserve, northeastern Durango. However, at any one time, most subadult and adult tortoises are associated with a single, active burrow (clean scraped sides, no debris). Thus, we think that it is reasonable to assume that each actively used burrow represents one live subadult or adult tortoise for one-time comparisons between different field surveys and study plots.

Hatchlings and small tortoises are difficult to find in all species of *Gopherus* (Douglass, 1978). These smaller individuals often use the burrows of other vertebrates or abandoned tortoise burrows. When they construct burrows, the burrows can be confused with rodent holes. Thus we consider our census information valid only for larger tortoises (>200-mm carapace length).

We first developed a generalized map of the region (Fig. 1), which emphasized the known and possible range of the tortoise relative to political boundaries, major towns, and primary routes of travel (road and rail). Next, we constructed a topographic map featuring identification of bolsons and mountains within the range of the tortoise plus adjacent areas (Fig. 2). These maps were based on

several sources, including information from Henrickson and Straw (1976) and United States–Mexican armed forces maps (1:250,000 scale). We quantified the size of tortoise districts by measuring their borders with calibrated thread, and calculated surface areas by superimposing “best-fitting” rectangles over the areas.

List of specimens.—We obtained the following by salvage of material (mostly shell fragments) found in the field or around human habitations. All material is deposited at the National Museum of Natural History.

COAHUILA. USNM 257966-968 (3 carapaces) Ejido Gregorio Garcia (Rancho El Socorro), 28 August 1981; USNM 257969 (bleached shell) Rancho La Mena, 4.8 mi E of, 7.7 mi W of El Socorro, 28 August 1981; USNM 257970-971 (carapace and plastron; different animals) Rancho El [=La] Mena, 12.5 mi W (by road) of El Socorro; USNM 257972-973 (2 plastrons) Rancho Berrinche (railroad tracks), 4.3 mi SSE of, valley is east of Cerro Solo, 7 April 1982; USNM 257974-979 (5 plastrons and 1 carapace fragment) La Vibora (at railroad tracks), about 6 mi (by road) SW of, about 25 (air) km ESE Los Americanos, 8 April 1982; USNM 257980 (carapace fragments) Rancho La Mena, 4.8 mi E of, road to Ejido Gregorio Garcia, 28 August 1981.

CHIHUAHUA. USNM 257981-985 (carapaces and plastron fragments) Rancho La Soledad, SE of Carrillo, 22 March 1982; USNM 257986-988 (3 carapaces) Rancho Peñoles, N of Rancho San Pedro, 22 March 1982; USNM 257989-990 (2 complete shells) Preson Peñoles, 3 km W of, about 19 km N of Rancho Arenales, 24 March 1982; USNM 257991 (carapace only) Ejido Division del Norte, near Sierra Los Remedios, 25 March 1982; USNM 257993 (fragments of carapace and plastron) Rancho Diana, 28 March 1982.

REGIONAL GEOGRAPHY

Gopherus flavomarginatus occurs only in a region often vaguely designated as the “Bolson de Mapimi.” Legler (1959) noted variance between sources using “Bolson de Mapimi” as a place name. Tamayo (1962) used this designation to cover most of the small closed and ephemeral drainages of extreme eastern Chihuahua and Durango, and west-central Coahuila. Van Devender and Burgess (1985) doubled the area of coverage by including the more southern drainages of the ríos Viga (Laguna de Palomas), Nazas, Aguanaval, and Salinas. Their definition unifies all of the internal drainages of the Chihuahuan Desert south of the Río Grande (and its subordinate Río Florida) and north of the Anticlinorium of Arteaga (the high transverse range of southern Coahuila) into a single unit. This approach offers conceptual consistency, but we do not use it here for several reasons:

(1) Resident Mexicans do not apply the term to this expansive area nor even to its northeastern half. Local usage and official military maps restrict “Bolson de Mapimi” to three drainages.

(2) Alternative, available regional names specify many of the areas in the inclusive Van Devender and Burgess (1985) definition: Llano del Guaje, Bolson de Cuatro Ciénegas, Bolson de Parras, Laguna de Viesca, and Laguna de Mayran. For example, the people of Torreón consider themselves as “Laguneros” and not dwellers in the “Bolson de Mapimi.” Further, in the vernacular usage “Bolson de Mapimi” is being replaced by “Zona de Silencio,” reflecting the remoteness of, and “mysterious” happenings in the area.

(3) Biogeographically, the adjacent bolsons in this region have different endemic herpetofaunas, for example, the Río Nazas drainage has several lizards (*Sceloporus jarrovi lineolateralis*, *S. ornatus caeruleus*, *S. maculosus*, *Uma exsul*, and *Xantusia henshawi bolsonae*) that do not occur within the “Bolson de Mapimi.” The latter region has *S. merriami* and *U. paraphygas*, which are sister species of *S. maculosus* and *U. exsul*, respectively.

We propose an alternative definition of the Bolson de Mapimi which satisfies most of these objections and considerations. The Mapimi Bolson system consists

Table 1.—*Tortoise sign recorded during surveys in 1981–82 in Bolson de Mapimi. Abbreviations: p-h (person-hr); Act (active); Inact (inactive).*

Date	Locality	Habitat or report	Transect		Total sign	Tortoise burrow				
			km	p-h		Live	Shell	Act	Inact	Scat
1981	Coahuila									
25 Aug	8 km S R. Palmira (=20 km S R. de Las Animas)	Creosote, mar- iola, tobosa; foothills	3	2	0					
	5 km S R. Palmira	Gramma and to- bosa	10	6	0					
	W Puerto del Jabali (E R. Las Animas)	Bajada, creosote; rocky foothills	1	3	0					
27 Aug	2 km W Rancho Las Animas	Open creosote	1	3	0					
	Near R. los Macheros (10 km W R. Las Animas)	Creosote, tobosa	1	4	0					
28 Aug	ca 5 km N of Los Americanos	Mesquite, creosote; near la- guna	1	3	0					
	2.4 km E R. La Mena (both sides from rd.)	Creosote, mes- quite, tobosa; flats	4	10	0					
	7.7 km E R. La Mena (ca. 12 km WSW El Socorro); N of rd.	Dense mesquite, creosote thick- et	2	5	23			1		22
	7.7 km E R. La Mena; S of rd.	Tobosa, creosote	2	5	1			1		
1981	Durango									
2 Sept	ca. 27 km SW Mapimi Reserve	Creosote, mes- quite, tobosa	2	10	6			1	2	3
	5 km SE Cerro San Ignacio	Grasses, creosote; sandy soils	1	4	3	1		2		
1982	Chihuahua									
24 Mar	N of Cerro Solo (24 km N Rancho Las Esperanzas)	Creosote, few mesquite and yucca	3	5	0					
	3 km W and 14 km N of Rancho Peñoles	Creosote, some mesquite and tobosa	1	3	5	1B	2	1	1	
	1.6 km N R. Trinidad	Creosote, tobosa, ocotillo, cacti	2	2.5	1			1		
25 Mar	ca. 8 km W of Rancho Peñoles	Tobosa, creosote, mesquite	5	4	1				1	
	S of R. San Isidro (10 km NW Carrillo)	Creosote, tobosa, mesquite	2	2	0					

Table 1.—*Continued.*

Date	Locality	Habitat or report	Transect		Total sign	Tortoise burrow				Scat
			km	p-h		Live	Shell	Act	Inact	
26 Mar	4 km NE Los Remedios	Creosote, yucca, agave, mesquite	2	1.5	0					
	1.8 km E R. San Miguel (NE Los Remedios)	Tobosa, cacti,	2.5	5	5				4	1
27 Mar	R. San Blas (30 km SSW Escalon)	Scrub, mesquite	2	5	0					
28 Mar	1.5 km W R. El Tepetate (SW Escalon)	Creosote, tobosa, mesquite	3	7	3			3		
2 Apr	Coahuila									
	5 km NE El Socorro	Creosote, mesquite, yucca	1	2	0					
	17 km SW El Socorro	Creosote, mesquite, some tobosa	1	1.5	0					
3 Apr	10 km W El Socorro	Tobosa, creosote, mesquite	2	1	0					
	2 km S, 5 km E La Mena	Tobosa, mesquite, creosote	2	3	5			1		4
	1 km E La Mena	Creosote, mesquite, some tobosa	2	4	2			1	1	
	4 km E La Mena	Creosote, mesquite, some tobosa	2	4	3			1	2	
12 Apr	0.5 km S, 8 km W Hwy. 49, on rd. to Jaralito	Tobosa, mesquite, creosote	1.5	2.5	0					
	12 km W Hwy. 49, on rd. to Jaralito	Tobosa, mesquite, creosote	1.5	2.5	0					

of a series of three contiguous, closed-drainage basins bounded by the Río Florida drainage to the northwest, the eastern versant of the Sierra Madre Occidental, and Río Nazas (Laguna Mayran) to the south and southeast. A series of limestone ranges, starting with the Sierra del Rey in the north, delimit the eastern boundary. The three bolsons are (Fig. 2): lagunas el Remolino, de Cerro Solo, and de las Palomas, Chihuahua; lagunas del Rey, Lagunillas, del Coyote, and de la Candelaria, Coahuila; and lagunas del Pato and de Puerto Rico, Durango.

Thus defined, the Bolson de Mapimi comprises a small segment of the Mapimian subprovince of the Chihuahuan Desert (Morafka, 1978). Even with the inclusion of small peripheral valleys (which harbor tortoises), the Bolson de Mapimi encompasses an area of about 71,000 km² (150 km in radius), centered just south of the Sierra Mojada in Coahuila (Fig. 2). The Bolson de Mapimi has one of the richest herpetofaunas of the Chihuahuan Desert, and a large number of endemic species, including the Bolson tortoise.

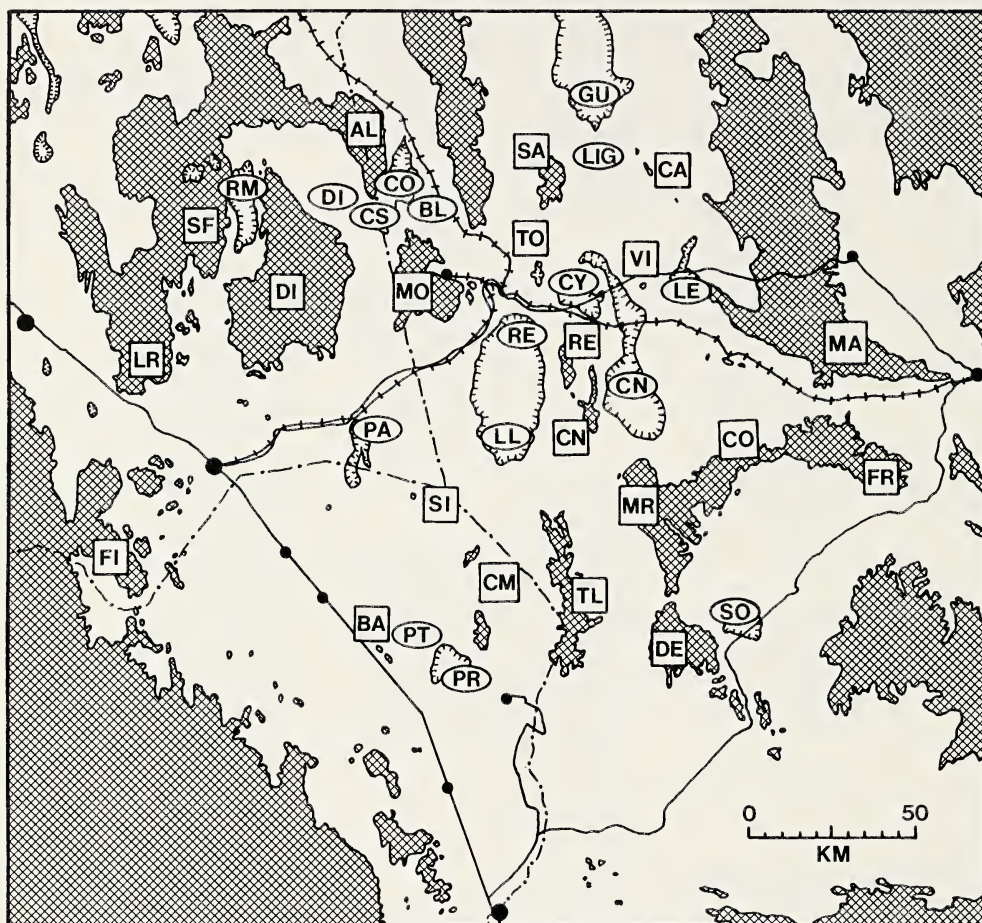


Fig. 2.—Map of major topographic features in and around the Bolson de Mapimi. Areas above 1500 m elevation are cross-hatched. Lagunas (L.), llanos and bolsons are coded in the ellipses: BL—Bolson de Lipanes; CN—L. de Candelaria; CO—L. Colorada; CS—L. Cerro Solo; CY—L. del Coyote; DI—L. NE of Sierra del Diablo; GU—L. del Guaje; LE—L. de la Leche; LIG—Llano del Guaje; LL—Lago Lagunillas; PA—L. de Palomas; PT—L. del Pato; PR—L. de Puerto Rico; RE—L. del Rey; RM—L. el Remolino; and SO—Valle de Sobaco. Mountain ranges (S = Sierra) and peaks (C = Cerro) are abbreviated in rectangles: AL—S. de Almagre; BA—S. Banderas; CA—S. del Caballo; CM—S. de la Campana; CN—S. de la Candelaria; CO—S. Colorada; DE—S. de las Delicias; DI—S. del Diablo; FI—S. de Felipe; FR—S. de la Fragua; LR—S. Los Remedios; MA—S. de la Madera; MR—S. de las Margaritas; MO—S. Mojada; RE—S. del Rey; SA—S. de San Antonio; SF—S. San Francisco; SI—C. de San Ignacio; TL—S. de Tlahualilo; TO—S. de la Tortuga; and VI—S. de la Vibora.

HISTORICAL DISTRIBUTION RECORDS

Legler (1959) states that "Dugès (1888; 1896) twice reported specimens of *Gopherus polyphemus* from Chihuahua. . . ." These records were probably overlooked for so long because of the similarity of the Bolson tortoise to the gopher tortoise (*G. polyphemus*) of the southeastern United States. The two tortoises are closely related, but distinct species. Also, the rarity of the tortoise in Mexico (especially along major roadways) and uncertainties about the early locality information caused delays in its recognition.

Further, Legler (1959) stated that the holotype (USNM 61253, adult; stuffed specimen with disassociated skull) was collected “30 to 40 miles from Lerdo, Durango, Mexico; . . . by Dr. Elswood Chaffee, 1918.” Lerdo is just west of Gomez Palacio and Torreón (now major cities, Fig. 1); all three are south of the known range of the tortoise. Legler and Webb (1961) stated the following:

Habitats in the immediate vicinity of Lerdo, Gomez Palacio, and Torreón seem to be unsuitable, and the species probably has been extirpated there by hunting and by encroachment of urban and agrarian development. Therefore, the somewhat indefinite type locality might logically be amended to read “30 to 40 miles north of Lerdo,” where suitable habitat exists . . . near La Campana . . . and just south of a mountain range bearing the same name. The locality “Lerdo” for one paratype [USNM 60976] could be interpreted in the same manner.

Auffenberg and Franz (1978) recognize Legler (1959) as the describer of the species but erroneously accept the type-locality as “30 to 40 miles north from Lerdo, Durango, Mexico.” Smith and Smith (1979) correctly report the original type-locality and the revision by Legler and Webb (1961).

The holotype and one of the paratypes (USNM 61254, same data) were possibly taken from the vicinity of the Sierra Banderas (north of Bermejillo and east of Highway 49; Fig. 1) or farther to the northeast nearer the Sierra de la Campana, Durango (Fig. 2). These sites are about 30–40 mi north of Lerdo. The tortoise is now extirpated or extremely rare in this region.

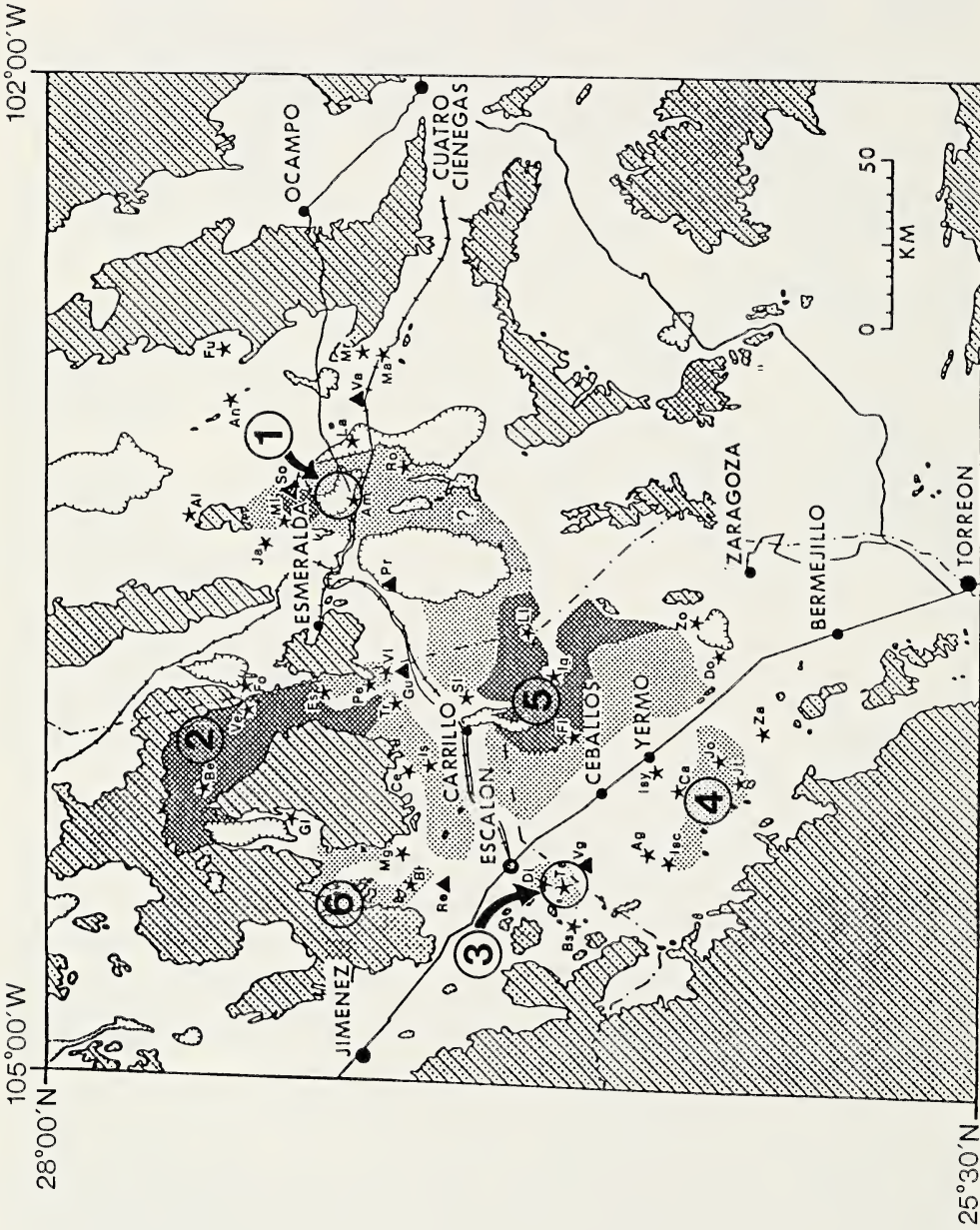
We do not think that the historical importance of this earlier series has been fully realized. If one of the paratypes (USNM 60976) was from Lerdo (as labeled), the range of the tortoise might have once extended farther south. There are no apparent barriers between the bolsons and foothills near the Sierra Banderas and the broad plain that includes Lerdo and Torreón (Fig. 2). Furthermore, if the two specimens (USNM 61253–61254) “30 to 40 miles from Lerdo” were taken in a direction other than north, then they may be from an area from which tortoises have not been reported. Most land in the Torreón region is now either heavily urbanized or developed as farmland, and we do not expect tortoises to persist there. However, we wonder whether unreported isolated colonies may remain on remote ranches south of its currently known range.

Also, Legler (1959) reported paratypes from Carrillo, Chihuahua (UIMNH 42953–42954, two carapaces, August 1958) and 8 mi east and 2 mi south of Americanos, Coahuila (KU 39415, carapace only, May 1954). Legler and Webb (1961) obtained nine tortoises east of Ceballos, Durango: 8 km east (UU 3572–3573, and five live tortoises; all September 1960) and 20 km east (MSUM 2251, KU 53806; both August 1959). Natives told them that tortoises occurred on the east side of the Sierra Banderas, Durango, and vague reports were obtained for “near Mapimi” [locality is unclear; it could be southwest of Bermejillo or east of Ceballos]. Persons in Ceballos indicated that tortoises were found both east and west of town, but that they were more common to the east.

Pawley (1968) vaguely reported a tortoise colony from “north of Torreón, a few miles from the nearest highway. . . .” Later, Pawley (1975) mentioned a large population near Sierra Los Remedios, Chihuahua.

Not including localities noted earlier, Smith and Smith (1979) provided a list of seven other museum records: CHIHUAHUA. Escalon; Ceballos, Durango, N of COAHUILA. Lilas, Rancho Las [adjacent to Durango border]; Socorro, Ejido, N Sierra de la Tortuga. DURANGO. Conejos, 10.2 km E; Chicahua [=Chihuahua?], nr. Ceballos; Flor, Rancho La; Mohovano, Rancho Aguaje San Ignacio.

Morafka et al. (1981) and Morafka (1982) summarized known museum locality



records and reports of the tortoise across its range, including latitude-longitude bearings. Many of these can be located on our new maps (Fig. 2–3).

CURRENT GEOGRAPHICAL DISTRIBUTION

The Bolson tortoise lives almost entirely in the valleys and low foothills of the Mapimi bolsons. The lagunas in the center of valleys are sometimes filled with water temporarily following late summer thunderstorms, which eliminates tortoises. Tortoises also occur to the west in the easternmost foothills of the Sierra Madre Occidental, areas which drain into the Mapimi lagunas. Outside of the Bolson de Mapimi, there is an extension of its range to the northeast near Laguna del Coyote, Coahuila (Fig. 2). Here, there is a broad opening to the Laguna de la Leche to the east and to the much larger lowlands of the Llano del Guaje. To our knowledge, there are some populations between Laguna del Coyote and the southern end of the Llano del Guaje, but none occur east to Laguna de la Leche.

The extant distribution of the Bolson tortoise occurs in a number of contiguous or adjacent bolsons (Fig. 3). We divide the range into six districts (Table 2), as follows:

District 1: Los Americanos, Coahuila

These are the northeasternmost localities for the tortoise. Populations occur to the west and north of Laguna del Coyote, a lake bed between the Sierra de la Tortuga to the west and the Sierra de la Vibora to the east (Fig. 2). A resident of Los Americanos told us he knew that “tortoises were no longer near town but occurred to the north throughout the Laguna del Coyote and northwest near Rancho Alazan [10 km north of Los Americanos].” Tortoises apparently have disappeared at Los Americanos and other areas near the rail line (which runs east to west from Cuatro Ciénegas, Coahuila, to Escalon, Chihuahua; Fig. 1) due to human predation. Earlier, one of us (Morafka) visited Rancho La Jarita, 18 km west-northwest of El Socorro, and locals did not know of any tortoises nearby.

On 28 August 1981 and 2–3 April 1982 (Table 1), we found much sign of tortoises (possibly representing several colonies) between Rancho La Mena (=Mina) to the west and Rancho El Socorro (now called Ejido Gregorio Garcia) to the east (Fig. 3). Residents have taken tortoises for food from these areas, based on tortoise

Fig. 3.—Map of *Gopherus flavomarginatus* distribution, showing study and survey sites. Solid circles mark cities and towns; triangles mark smaller towns, as follows: Gu—Guimbaleté; Pr—Providencia; Re—Los Remedios (Ejido Division del Norte); So—El Socorro; Va—La Vibora; Vg—Vicente Guerrero. Stars indicate ranchos and smaller ejidos, as follows: Ag—San Agustín; Al—San Antonio de los Alamos; Am—Los Americanos; An—Las Animas; Be—Benthon; Bl—Palo Blanco; Bs—San Blas; Ca—El Canelo; Ce—Cerros Blancos; Di—Diana; Do—San Dionisio; Fl—La Flor; Es—Las Esperanzas; Fo—Fortuna; Fu—El Fuste; Gl—La Gloria; Ig—San Ignacio; Is—San Isidro; Isc—San Isidro del Derrame; Isy—San Isidro de Yermo; Ja—La Jarita; Jl—El Jaralito; Jo—San José; La—Lagunilla; Ll—Las Lilas; Ma—Magueyal; Mg—San Miguel; Ml—La Mena; Mr—Mirador; Pe—Peñoles; Ro—El Cinco; Sl—La Soledad; Te—Tepetate; Tr—La Trinidad; Ve—La Ventura; Vi—La Victoria; Za—La Zorilla; Zo—La Zorra. Unbroken lines are major roads; cross-barred lines are railroads; dot-dash lines are state boundaries. Lagunas and playas are indicated by encircling lines hatched on the inside; cross-hatched areas are above 1500 m elevation. Tortoise distribution is indicated by light (low density) or heavy (high density) stippling.

Table 2.—*Analysis of factors responsible for limiting Bolson tortoise distribution.*

Districts	Area (km ²)	Perimeter (km)	Perimeter/ area	Percent of perimeter		
				Extir- pation	Relief	Playa
1. Americanos, Coah.	1000	180	0.18	10	30	60
2. Diablo, Chih.	2000	330	0.17	30	60	10
3. Diana, Chih. (west of highway)	65	30	0.58	60	40	0
4. Yermo, Dur. (west of highway)	100	50	0.5	100	0	0
5. Mapimi (Reserve) Dur., Coah., Chih.	2425	370	0.15	60	20	20
6. Remedios, Chih.	500	80	0.16	40	40	20
Totals	6090	1040	0.17	42	36	22

shells obtained in El Socorro by Morafka et al. (1981), Morafka (1982), and our location of shells here and at La Mena. Three cowboys interviewed in El Socorro on 28 August 1981 said that "tortoises occur west and southwest of town." A resident at Rancho La Mena said that "tortoises are present here, but the ones they had eaten [shells found in trash] were from El Socorro to the east." However, on our survey at 7.7 km east of Rancho La Mena in August 1981, we found 22 tortoise scats in a mesquite thicket plus several soft drink bottles, suggestive of human visitation to obtain tortoises. On 2 April 1982, we observed one excavated burrow 1 km east of La Mena. It was 20 m north of the dirt road (La Mena to El Socorro); the burrow reached 1 m deep and curved to the left (semi-circle). A local cowboy visited our camp during our survey of a 25-ha plot (1.8 km south of the La Mena-El Socorro road and about 5 km east of La Mena), and he related that tortoises were becoming uncommon in this valley but they are still eaten when found.

On 25 August 1981, we did not find any tortoise sign during surveys near Rancho Palmira, 30 km east-northeast of El Socorro (Table 1) nor did we learn of any tortoises from residents at Rancho Las Animas, 30 km northeast of El Socorro. An elder at Rancho El Fuste (10 mi northeast of Rancho Las Animas, foothills of the Sierra Madre Oriental) said that "tortoises are known from Americanos to the southwest of El Fuste; they are not here, to the north nor east."

We returned to Rancho Las Animas and on 27 August 1981 crossed the southern end of the Sierra del Caballo in order to reach Rancho Los Macheros (10 km west of Rancho Las Animas), which is located in the eastern foothills of Sierra la Chorrera. We were unable to locate Los Macheros because new PEMEX exploration roads criss-crossed the valley, and local traffic had shifted to these better roads. We surveyed parts of the area without finding any tortoise sign (Table 1), but we cannot state conclusively that tortoises are absent. We know that tortoises occur near El Socorro, and they apparently disappear somewhere between there and areas 30 km to the northeast (approaching the Llano del Guaje).

Southeast of Los Americanos, we recorded tortoise sign or received reports of tortoises at three new localities (Table 1). At Rancho Lagunilla (15 km east of Los Americanos and 7 km south of main gravel road from Esmeralda to Ocampo), a rancher said that "tortoises are present here but rare." At Rancho Berrinche (=Rancho Matrimonio Viejo), 11.7 km south of Rancho Lagunilla, a rancher reported "tortoises present to the south in a large open valley." We found tortoise remains (mostly plastrons) in trash piles at two sites south of the railroad line: 7 km south-southeast of Rancho Berrinche and about 14.7 km west of Magueyal (Table 1). A broad valley extends south of this area and it may contain tortoises; the southern terminus of the range is the Sierra Colorada (Fig. 3).

On 8 April 1982, we inquired at Hacienda Magueyal (44 km east-southeast of Los Americanos; Fig. 3), along the railroad line, and a local resident reported that “there were no tortoises east of La Vibora [29 km east of Los Americanos], but they are at Rancho Palmira to the north [about 32 km north of Magueyal].” Earlier (25 August 1981), we found no evidence of tortoises near Rancho Palmira, but further searching is warranted. In 1982, we visited both Rancho Mirador (4 km northeast of Magueyal) and Rancho Poma (15 km north of Magueyal or 7 km south of Puertecitos on main gravel road Esmeralda-Ocampo), and cowboys at both ranches reported “no tortoises in this valley nor to north; they occur to the west.” These reports and our surveys suggest that the eastern limit of the tortoises’ range is west of La Vibora, Coahuila (Fig. 3).

District 2. Sierra del Diablo Region, Chihuahua

This is a long, broad valley situated between the Sierra Mojada–Sierra de Almagre to the east and the Sierra del Diablo to the west. Tortoises occur northward at least to Rancho La Ventura and then westward to Cerros Emilio (low hills rising from the bolson floor), nearby Preson Tortola, and near foothills of the Sierra del Diablo southeast of Rancho Benthon (Fig. 3).

East of Rancho La Ventura, we have not found or received any reports of tortoises (Table 1). On 24 March 1982, we interviewed residents about tortoises in this region. On the road halfway between Cerro Solo in Chihuahua and Laguna Colorado, 10–15 km to the northeast in Coahuila, one cowboy said that “there are no tortoises nearby, but they are present to the northwest at Rancho La Ventura and west of Cerro Solo.” Near Rancho Fortuna, Coahuila (6 km east of Rancho La Ventura; Fig. 3), a rancher reported “no tortoises at his ranch nor to the east around Bolson de Lipanes, or to the south at Laguna Cerro Solo; they are present to the south at Rancho Las Esperanzas.” In 1969, one of us (Morafka) visited ranchos Hormigas (29 km north of La Ventura) and Jaco (50 km north of La Ventura), both in Coahuila, but residents did not know of any tortoises there.

We found shells, burrows and one tortoise (in burrow) at or near ranchos Las Esperanzas, Peñoles, La Trinidad, and La Victoria (Table 1); these sites are in the main bolson south of Rancho La Ventura and north of the railroad line, in Chihuahua. The resident at Rancho Las Esperanzas reported no tortoises nearby, but another resident said “tortoises had been eaten at this ranch.” At Rancho Robles, near Rancho La Victoria, a cowboy said that “the ranch owner has given strict orders that tortoises are not to be taken here. Numbers locally have been depleted by people from Carrillo [25 km to the southwest] who take them.”

Tortoises probably once were distributed continuously from the Sierra del Diablo population westward to the Sierra Los Remedios (District 6), but human removal and agricultural activities have depleted or extirpated most of these colonies. A resident at Rancho Cerros Blancos, about 25 km northwest of Carrillo, reported that “tortoises were in the general area, mostly to the north in Sierra Los Remedios area.” We found no tortoise sign in a brief survey near Rancho San Isidro, 10 km northwest of Carrillo (Table 1). There are many roads and farms in the area.

District 3. Rancho Diana, West of Highway 49, Chihuahua

There were previously no documented records of the tortoise west of Highway 49. However, Rancho Diana and surrounding ranches southwest of Escalon may constitute a small fragment of the tortoise’s range. The area is bordered to the south by the state line (artificial demarcation), but just south of there is a major

agricultural area accessed by a paved road running westward from Ceballos and parallel (20 km south) to the Chihuahua-Durango border.

On 3 September 1981, we visited Ejido Vicente Guerrero (Rancho Chalella), Durango (approximately 25 km south of Escalon by air) and were directed to a house where two tortoises were being kept alive. The owners were reluctant to talk but upon sharp questioning they said that "these tortoises were from Rancho Diana, Chihuahua. They didn't mean them any harm, and were keeping them as pets." They agreed to return the tortoises to their native habitat.

On 27–28 March 1982, we explored southwest of Escalon. At Rancho El Tepetate, the ranch foreman told us that "tortoises were present between the ranch house and low hills west of the ranch; he recently saw one there, but he had no tortoises or shells at his house." We subsequently found three burrows 1.5 km west of the ranch (Table 1). Just to the south at Rancho Las Adjuntas (6.7 km northwest of Ejido Vicente Guerrero), a resident reported that "tortoises were found nearby many years ago; he had caught and released one to the northwest at the base of the hills; no other tortoises known recently."

Finally, on 28 March 1982 we reached Rancho Diana (9 km by road north of Rancho Las Adjuntas), Chihuahua. The ranch is 14 km south-southwest by air from Escalon. Here we found tortoise remains in a garbage dump (Table 1). A local resident did not want to say who was eating them, probably because we were accompanied by biologists of Mexico's wildlife department. However, upon questioning, he reported that "tortoises are scarce here; he saw one live adult about three months earlier. They may live to the north [not sure]. Chacone ranch to the north is better for tortoises than here." We could not find Rancho Chacone, and it probably is a new local name. Rancho Diana is on the east side of Cerro de la Chorrera, and the habitat is rolling foothills. We do not know if the tortoises were actually collected there or downslope, where the soils are more alluvial. These records document tortoise occurrence in what is probably the northwesternmost part of the range.

District 4. Ceballos to Yermo, West of Highway 49, Durango

There are broad plains and rolling hills west of Highway 49 and south of the Durango border. However, the paved highway (west from Ceballos) divides the area. This part of Durango has extensive farmland on most lowlands, and ranches in the foothills.

On 31 August 1981, we visited Rancho San Isidro, about 5 km west of Yermo (on Highway 49). Here, a gentleman (76 years old) summarized the status of tortoises locally as follows:

"Tortoises are present in low foothills 12–13 km west of Yermo, but they are very rare now. Tortoises were in this valley [lowlands east of foothills] many years ago, but workers on the highway and railroad cleaned them out. Mule-drivers worked the area in the 1920s, turning the land into agricultural fields. In those days, they would take 10–15 big tortoises each week as food for Saturday night fiestas. The chief mule-driver would save the largest tortoise for himself and have it for breakfast. Tortoises do not extend much farther south than immediately west of this rancho, and to low hills to the south [near Rancho El Canelo]."

He said that it was a long time since anyone had seen a live tortoise, but this year his son had found two tortoises along a new PEMEX exploration road about 3–4 km due west of the ranch. The tortoises were at the ranch for awhile, but they were taken away to breed with others in Bermejillo. He took us out to the general vicinity, and the habitat was foothills with low scrub.

On 3 September 1981, we visited several ranches west and north of Ceballos, Durango. El Diamante (27 km southwest of Ceballos) was in the rocky foothills, and a resident said that "there are no tortoises here." In agricultural fields near Rancho San Gerardo (14 km west of Ceballos), field workers related to us that "tortoises live to the west in the foothills and north at Rancho Diana."

On 12 April 1982, we explored west of Highway 49 and south of Yermo but observed no tortoise sign. There is an extensive tobosa grassland west to Rancho San Jose and Rancho Jaralito. At Rancho San Jose, a cowboy informed us that "there are no tortoises present on this side of the Sierra Banderas, which are hills due east and on the other side of Highway 49. Tortoises are present in that region but people there don't respect their fauna. If tortoises were ever present here, they have been gone a long time." To the south of these areas at Rancho Zorilla, two local men said that "there are no tortoises on this side of the highway, but they occur on the other side." Also, we briefly traveled west from Ceballos for interviews. A cowboy at Rancho San Agustin, 25 km west of Ceballos on the road to Parral, stated that "tortoises occur throughout this valley but farther to the south in low hills and to the west. They are now scarce. The few left are still eaten by people." At Rancho San Isidro del Derrame, 6 km southwest of Rancho San Agustin, a man said he saw one tortoise here about three years ago, but he didn't know where it came from. An elder of the village provided a synopsis for us:

"Tortoises are over the next row of small hills to the east, and from there they range to the east somewhat and to the north. The southern limits are in lomas near Rancho El Canelo southwest of Yermo. There were many tortoises here at one time but everyone has persecuted them."

Both elderly gentlemen at ranchos San Isidro (one west of Yermo and the other west of Ceballos) indicated that the southwestern limit of the tortoise distribution occurs in lomas and foothills near Rancho El Canelo, about 12 km southwest of Yermo. These are corroborative, compelling testimonies about the occurrence and demise of the Bolson tortoise in the western part of its range.

District 5. Mapimi Core Region, Durango-Coahuila

East of Highway 49 and south of the east-west rail line (Escalon to Cuatro Ciénegas) lies the largest area occupied by Bolson tortoises. This is mostly open terrain with small lagunas, sandy lomas, rolling low hills and a few rocky uplifts.

Tortoise populations occur eastward from Highway 49 through at least Rancho San Ignacio (and the nearby MAB Mapimi Reserve) in Durango, and to Rancho Las Lilas at the Durango-Coahuila border. Tortoises extend east to the foothills of the Sierra de la Campana, a large north-south range, but their local distribution here and across plains northeast of Rancho Las Lilas is poorly documented.

On 2 September 1981, a resident at a remote ranch, 14 km south of Las Lilas, indicated that tortoises occur on low hills (Lomas del Venado Gaucho) to the southeast. Here, we found some tortoise sign (Table 1). We attempted to explore to the southwest (toward Lomas del Canelo) but roads were impassable due to recent rains. On our return trip, we found a live tortoise (250-mm carapace length) crossing a dirt road 5 km southeast of Cerro San Ignacio (Fig. 2). A burrow was found 20 m east of the dirt road, and on the west side of the road we found another burrow.

The southern terminus of the tortoise's range in the Mapimi Core District is unclear (see Historical Distribution). On 20 August 1981, we visited near Ejido La Campana (on the road to Tlahualilo de Zaragoza) at the south end of Sierra

de la Campana, Durango (Fig. 2-3, and a cowhand (64 years old) recounted the history of the species:

"Tortoises were much farther south than at La Campana. They once occurred in this area, and even south of the road [pointed to main gravel road from Est. Conejos on Highway 49 to La Campana]. But, tortoises were all eaten many years ago when I was a child. They are now all gone locally. A permit is needed to collect them as they are legally protected."

We returned to this region on 11 April 1982 to conduct more interviews. We first stopped at Rancho San Dionisio, 9.6 km northeast of Highway 49 (at Tlahualilo turnoff, 34 km north of Bermejillo). A local said that "tortoises are present to the west in foothills of the Cerro del Indio. Some were taken there two months ago but they were returned. Also, tortoises are at Rancho La Zorra to the east of here." Cerro del Indio is less than 5 km east of the Sierra Banderas, which is about 5 km east of and parallel to Highway 49. Cowboys at Rancho La Zorra, 21 km east-northeast of Highway 49 (Tlahualilo turnoff), stated that "tortoises were present in Lomas del Canelo, north of Rancho La Zorra, but they are mostly gone due to candelilla workers who have taken most of them. Tortoises are absent south of here."

The habitat in the La Campana-La Zorra region is varied, including creosote and mesquite shrubland mixed with tobosa flats. There are a few small lagunas in the middle of basins. Foothills and mountains are generally within view. There are no major ranches between La Zorra and Las Lilas (50 km to the north) and east of Highway 49 from the Sierra Banderas north to Yermo, which are 20 km apart (Fig. 3). Several large arroyos and sandy soils (and associated lomas) occur in this region, perhaps rendering it less suitable for agriculture than other lands. There reportedly are tortoise colonies in the Lomas del Canelo and adjacent flats, and further surveys are needed in this large, relatively uninhabited area. It is an area where animals could be protected.

The largest known populations of tortoises are northwest of Cerro de San Ignacio, about 35 km east-northeast of Ceballos (on Highway 49), and some of these are now in part of the MAB Mapimi Reserve. Local residents are keenly aware of the protected status of tortoises on the Reserve and they assist in safeguarding these colonies.

District 6. Sierra Los Remedios Region, Chihuahua

The northwesternmost populations of the tortoise occur in the valley between the Sierra del Diablo and Sierra Los Remedios to the west (Fig. 3). To our knowledge, tortoises have not been found at Rancho La Gloria or around Laguna El Remolino north of the Los Remedios area. We have only learned of tortoises in the southern part of the valley. We surveyed this area on 25-26 March 1982, finding new material and reports of tortoises (Table 1).

At the small town of Los Remedios (Ejido Division del Norte) a resident reported "tortoises were present on flats below the ejido [to the east] and in the adjacent large valley to the northeast; none were up the narrow canyon to the northwest of town." A local resident took us to an active burrow about 4 km northeast of town. He stated that "most tortoises here had been eaten and they were once larger in size." He thought there might be more tortoises farther up the valley. A truck driver told us that tortoises were on the other side of the valley at Rancho San Miguel, and "there were once lots of tortoises farther down [south] in this valley, but there are not many now."

Interviews with locals on the west side of the valley indicated that none were present. At Ejido Alejandro Carrillo, 13 km north of Los Remedios (near Rancho Palo Blanco; Fig. 3), a resident reported that "they were once just to the east of the ejido over a cerro [hill] but they are now very scarce." In Ejido Texcoco (17 km north of Los Remedios) a resident stated that "tortoises are in the valley to the east and people eat them in this ejido; however, there are no shells presently available." At Rancho San Miguel (7 km east, 17 km north of Los Remedios), the resident initially was reluctant to discuss tortoises, but eventually said that "tortoises are in this valley and to the north. They come out in the rain. Tortoise is very good to eat but you must have the permission of the owner to kill one." One shell was found in their trash pile (Table 1).

TORTOISE ABUNDANCE AND SPATIAL PATTERNS

We determined the numbers and spatial patterns of burrows and other sign at two 25-ha plots: near El Socorro, Coahuila (Fig. 4) and Cerros Emilio, Chihuahua (Fig. 5–6). In addition, Gustavo Aguirre kindly provided comparative data from his study area (76 ha) at the MAB Mapimi Reserve, Durango (Fig. 7–8). Ing. Jose Treviño and Pablo Dominguez allowed us to use their information from three 25-ha plots in Chihuahua (Fig. 9–11). The number of burrows differed markedly between these sites (Table 3), ranging from no active burrows/ha at Ejido Emiliano Zapata, Chihuahua, up to 0.50 at the Mapimi Reserve. There appear to be colonies (nuclear areas) at Cerros Emilio (Fig. 6), the Mapimi Reserve (Fig. 8), and Rancho Las Esperanzas (Fig. 11).

We found few burrows on the El Socorro plot (Fig. 4). They occur in grass and low bushes at the edge of open areas. Two are adjacent to expanses of desert pavement (hardpan, embedded gravel). Although we obtained indications of tortoise abundance in this area based on walking surveys (Table 1), few sign were on our plot. We either located the site in a poor habitat, or in an area that had been depleted by tortoise hunters.

The Cerros Emilio plot we surveyed has packed clusters including 11 active and 33 inactive burrows (Fig. 6). About 60% of the active and inactive burrows are concentrated in only 15% of the area. Here and elsewhere, however, there are occasional single burrows away from the clusters.

Aguirre et al. (1984) employed telemetry to follow tortoises through dry and wet seasons at the Mapimi Reserve. They discovered that tortoises move directly from one burrow to another, apparently knowing the location and direction to burrows. There was almost no immigration of adults from another cluster, even when adjacent clusters are contiguous (G. Adest, personal communication). The home ranges of male tortoises do not overlap and they display a possible dominance hierarchy. Aguirre et al. (1984) concluded that clusters of burrows in the Mapimi Reserve represent socially organized colonies.

Most burrows in the Mapimi study area appear to be near vegetation (Fig. 8). We divided the location of burrows into two categories based on their nearest distances to shrubs (creosote, mesquite) or tobosa grass. We found 32 burrows (68%) inside ($N = 12$) or at the edges ($N = 20$) of shrub habitat; five more burrows within 5 m, six from 10–30 m away, and six from 100–185 m away from shrubs. Six burrows were inside or at the edge of tobosa, and five burrows were 5–10 m away from tobosa. For shrub and tobosa together, 66% of the burrows were in or at the edge of vegetation (about 76% of the burrows within 5 m of vegetation).

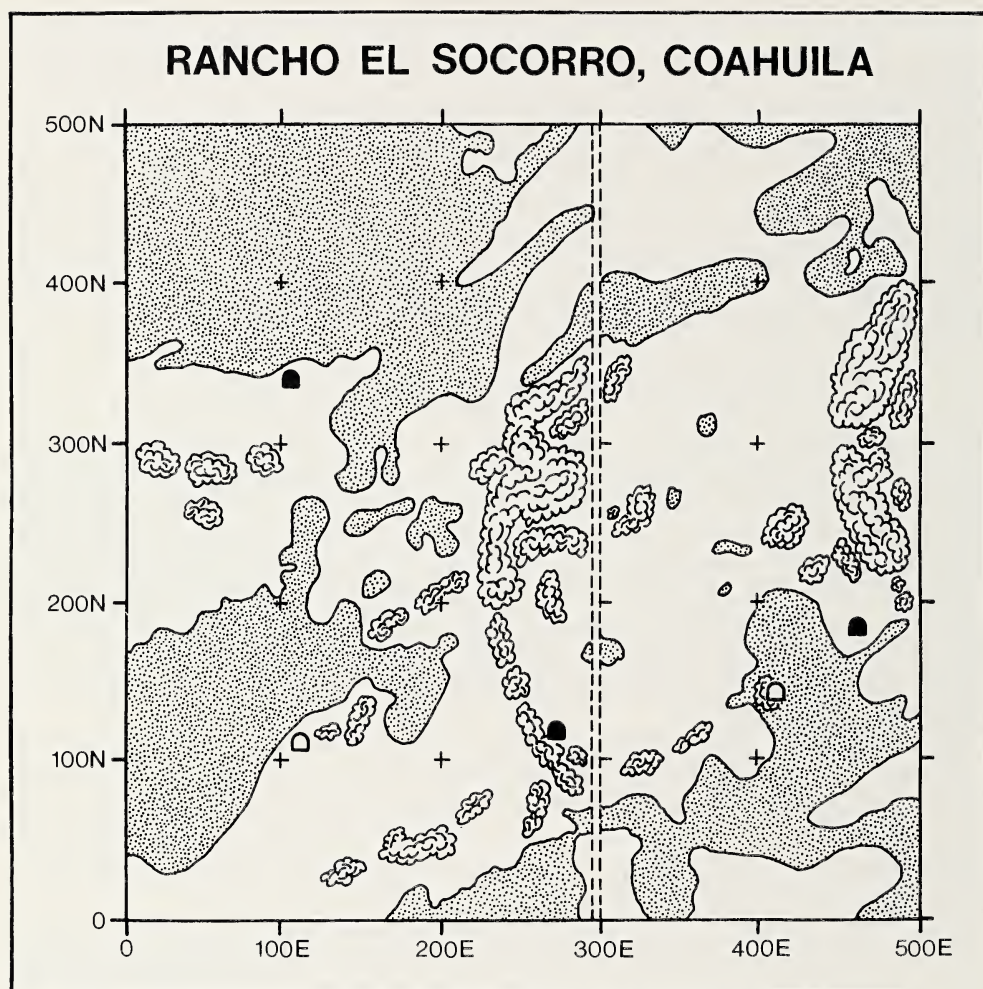


Fig. 4.—Twenty-five hectare plot census of burrows near Rancho El Socorro, Coahuila.

Ing. J. Treviño and P. Dominguez found only three abandoned and two caved-in burrows at Ejido Emiliano Zapata (Fig. 9). Their survey near Cerros Emilio revealed four active and one abandoned burrows (Fig. 10). A colony may occurred earlier at Rancho Las Esperanzas based on the occurrence of nine caved-in burrows in 1 ha (Fig. 11); there are also two inactive, three active and two occupied burrows.

A general calculation of the total number of tortoises can be inferred from an estimation of burrow abundance. The high density or "nuclear" patches appear to be confined to only about 1% of the inhabited range. Aguirre et al. (1984) suggested an average density of 3.0 tortoises (burrows)/ha for nuclear areas and only 0.1 tortoise/ha in non-colonial populations or at the periphery of colonies. On a larger scale, these values are 300 and ten tortoises/km², respectively.

The total area of tortoise occurrence for all six districts is estimated to include 6090 km² (Table 2), which is considerably less than earlier estimates of 50,000 km² (Morafka, 1982; Morafka et al., 1981). Even within this reduced area, tortoise occurrence is mostly restricted to the upslope borders of bolsons. Thus, the area



Fig. 5.—Photograph of habitat at census site 1, Cerros Emilio, Chihuahua.

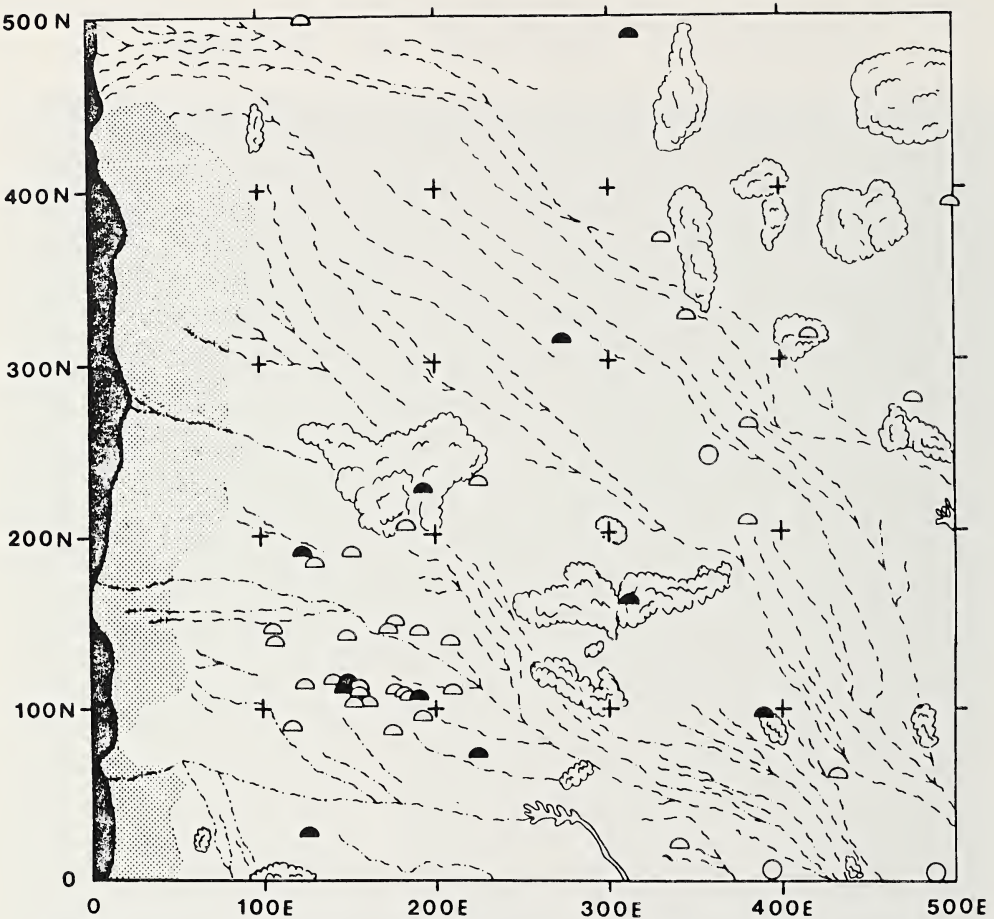


Fig. 6.—Twenty-five hectare plot census of burrows at site 1, Cerros Emilio, Chihuahua.

actually occupied by tortoises is probably smaller by an order of magnitude (about 700 km²). At an average density of ten tortoises/km², the number of tortoises is 7000. Perhaps ten nuclear colonies remain with 300/km², which could add another 3000 individuals. Altogether, there may be no more than 10,000 adult-sized tortoises remaining in the Bolson de Mapimi.

LIMITS AND ISOLATION OF POPULATIONS

The major factors affecting the spatial distribution of *G. flavomarginatus* are artifacts of recent human intrusion, working in concert with natural isolation. We measured the boundaries between the six districts based on three criteria (Table 2): (1) human presence or extirpation of tortoises (related to nearby roads, ejidos, ranches or villages); (2) known laguna boundaries (tortoises do not occur in flooded areas); and (3) exposed limestone ridges (uninhabited by tortoises). Other factors such as soil, climate, and vegetation are not strongly coincidental with the boundaries of tortoise distribution (Morafka, 1977; Lieberman and Morafka, this volume). Overall, areas with human occupation account for 42% of the fragment borders, followed by ridges (36%) and lagunas (22%).



Fig. 7.—Photograph of habitat at the Mapimi study site, approximately 10 km north of the Laboratorio del Desierto (50 km ENE Ceballos), Durango.



Fig. 8.—Seventy-six hectare plot census of burrows at the Mapimi study site.

Human disruption is clearly evident as the major isolating factor of extant populations. We established the districts based on obvious fragmentation of the tortoise's range by human development (farms, ejidos, roads, railroad lines) and, in turn, human predation on colonies.

The western part of the tortoise's range is defined by Highway 49, dividing the western districts from all the others. Farms occupy most of the area 10 km on each side of the main highway from Escalon, Chihuahua, south for 65 km (about 15 km south of Yermo, Durango). District #3 (Rancho Diana) and District #4



Fig. 9.—Twenty-five hectare plot census of burrows at Ejido Emiliano Zapata, Chihuahua.

(Yermo) are separated from one another by intervening tilled land, and the paved highway from Ceballos west to Parral.

The northwestern area (District #6: Los Remedios) is an outpocket from the Mapimi core (District #5). Tortoises have been severely depleted in a zone about 10 km wide on either side of the rail line from Escalon (at Highway 49) to Carrillo, 45 km to the east (Fig. 3), which now isolates Los Remedios tortoises from the Mapimi core.

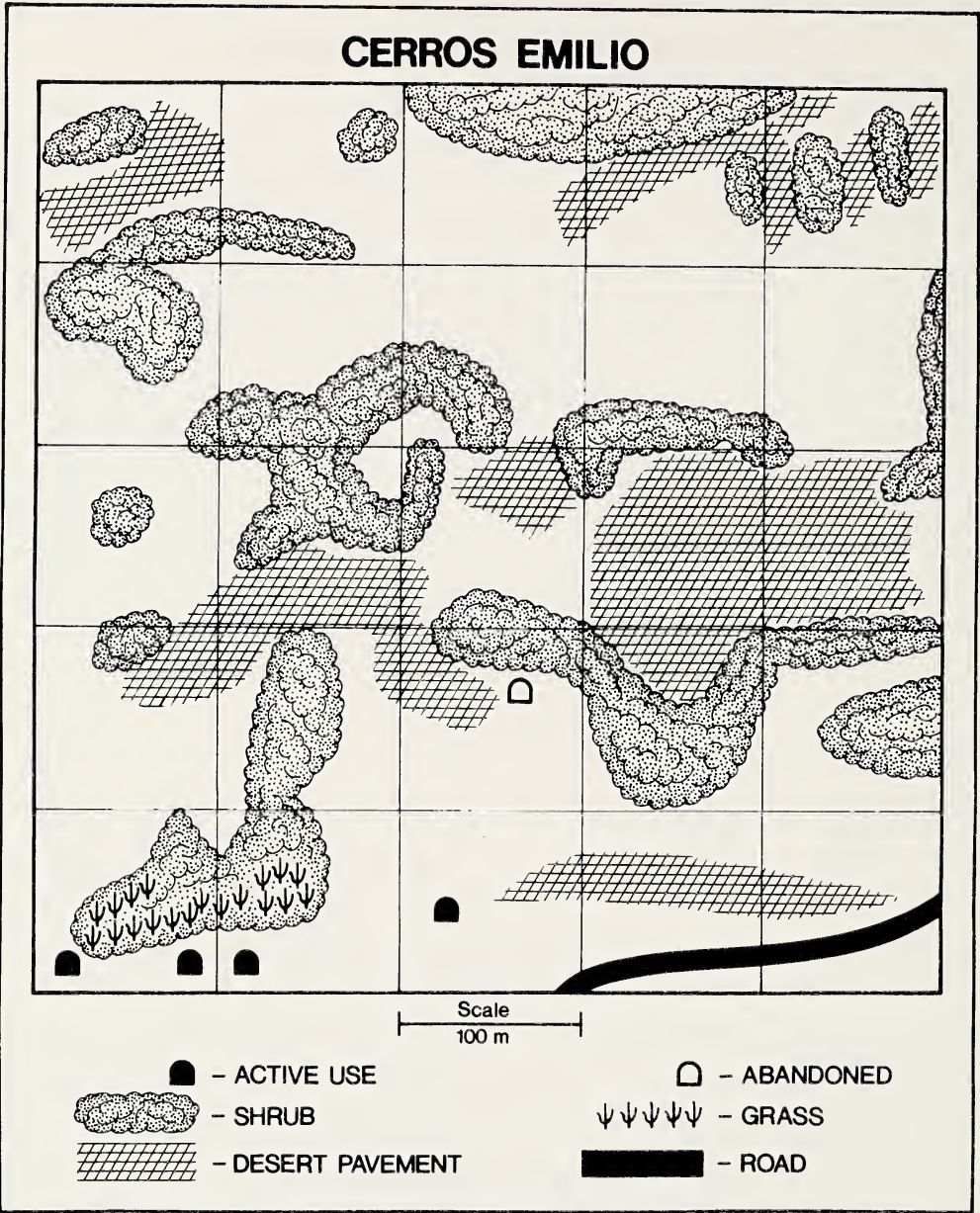


Fig. 10.—Twenty-five hectare plot census of burrows at site 2, Cerros Emilio, Chihuahua.

The northeastern populations (District #1: Los Americanos) may have been continuous with tortoises to the southwest (District #5: Mapimi core) through an area at the north end of Laguna del Rey. We do not know of any extant colonies in this area, which is now occupied by Ejido Providencia, railroad lines and roads (such access probably has led to local extirpation of colonies). Alternatively, the convergence of the ancient shorelines of Laguna del Rey with the limestone ridges

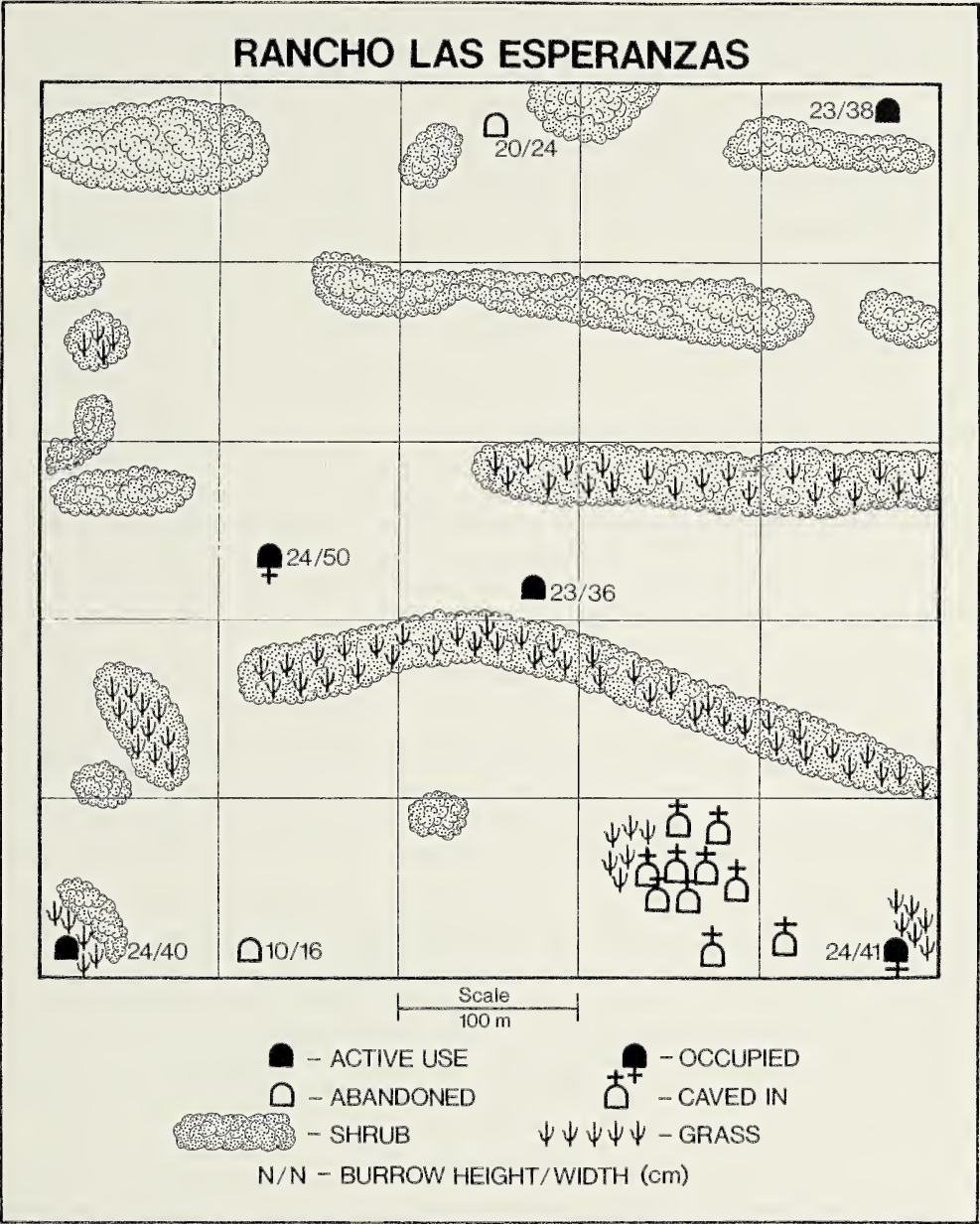


Fig. 11.—Twenty-five hectare plot census of burrows at Rancho Las Esperanzas, Chihuahua.

of Sierra del Rey and Sierra Mojada may have formed a natural bottleneck or barrier to dispersal through this area (Fig. 2).

The rail line with adjacent roads and settlements separates the Mapimi core from the Sierra del Diablo populations (District #2; Fig. 3), but there may have been other isolating factors in this area. About 30 km to the south, a series of

Table 3.—*Comparison of tortoise burrows at six study sites.*

Locality	Area (ha)	Total N burrow		Active burrows per ha
		Active	Inactive	
Coahuila				
El Socorro	25	3	2	0.12
Durango				
MAB Mapimi Reserve ¹	50	24	—	0.50
Chihuahua				
Cerros Emilio	25	11	33	0.44
Ejido Emiliano Zapata ²	25	0	5	0
Cerros Emilio ²	25	4	1	0.16
Rancho Las Esperanzas ²	25	5	12	0.20

¹ Data courtesy of G. Aguirre.

² Data courtesy of J. Treviño and P. Domínguez.

lagunas, arroyos and low valleys run west-to-east parallel to the railroad. In particular, flooding during interglacial periods of the Holocene may have connected Laguna de Palomas in the west with Laguna del Rey to the east (Fig. 2), thereby severing or restricting connection between the northern populations (Diablo) and the southern ones (Mapimi core).

Observed morphological differences between Diablo and Mapimi populations support this hypothesis. Typically, Diablo tortoises have little yellow on the carapace and, when present, it is usually confined to the marginals; in the Mapimi core area, tortoises often have extensive yellow coloration. Landers et al. (1982) described a similar latitudinal shift from a northern, dark carapace to a southern, light carapace (yellow) in *G. polyphemus*. They attributed adaptive significance to the changes based on reduced reflectivity in cooler, more northern localities. However, it is difficult to explain the differences in coloration given the small distance between populations of *G. flavomarginatus*.

Diablo tortoises are also larger in body size, have distinctive scute anomalies, and males show more concavity in their plastrons compared to those from the Mapimi core (Morafka et al., 1981). However, electrophoretic comparisons of blood proteins fail to confirm any major differences in alleles among 20 presumptive loci in *G. flavomarginatus* (R. Murphy, personal communication). To date, most sample sizes have been small (except from the Mapimi core area) and further work is needed to clarify the level of geographic morphological variation in this species.

STATUS

At present, there is no evidence of the existence of any colony with substantial numbers in the western part of the tortoise's range. Their continued existence in this area may be in immediate jeopardy because of the vulnerability of the small, isolated populations (or individuals) and increasing human occupation of habitat. We do not know how far tortoises range to the north or to the west in the western foothills region, but we doubt they will be found much beyond the areas delimited here.

Future work should focus on efforts to locate and protect remaining pockets of tortoises occurring in western populations near (1) El Canelo, southwest of Yermo, Durango; (2) Rancho Diana, southwest of Escalon, Chihuahua, and (3) northeast

of Los Remedios, Chihuahua. These populations are especially important because they may live in different habitats than are currently known (e.g. in foothills or sandy lomas), and may represent isolated genetic stocks relative to the Mapimi core area.

The western and northwestern areas of the range may already lack populations of minimum viable size (self-sustaining populations with sufficient numbers to avoid deleterious inbreeding effects or chance extinction). For example, there may be less than 50 pairs of adult tortoises remaining west of Highway 49. These isolates could easily be lost.

We do not know the status of tortoise populations from the Lomas del Canelo (east of Highway 49), Durango, northeast to Las Lilas and farther east of the Durango-Coahuila border. This region merits further surveys because these are isolated areas where colonies may still be intact. There are records of tortoises near Las Lilas and west of La Vibora, Coahuila (Fig. 3), but there is a need to document their occurrence in the intervening area south of the railroad near Lago Lagunillas, Sierra de la Candelaria, and Laguna de la Candelaria (Fig. 3).

Our surveys and interviews suggest that tortoises on either side of the Sierra del Diablo are now isolated from one another, and probably also from the Mapimi core area to the south. At one time, these populations likely were continuous with the other districts. The Mapimi and Sierra del Diablo districts are two large adjacent areas, together including about 73% of the total known range of the tortoise.

Populations are protected at the MAB Mapimi Reserve in northeastern Durango. Mexico's wildlife department and private conservation agencies are presently attempting to establish two protected areas on ranches in the Sierra del Diablo region, southeastern Chihuahua. The ranchers already prohibit disturbance of their tortoise colonies. We recommend a third protected area at the northeastern limit of the tortoise's range, between La Mena and El Socorro, Coahuila. Although there are indications of some sizeable colonies here, tortoises were being taken in 1981–82.

While we estimate that about 10,000 adult tortoises still exist, we caution against speculation that there are many large colonies remaining in the wild. We have visited almost every area known to harbor tortoises, and most of these sites have been subjected to harvesting of tortoises in the past. Knowledgeable residents have directed us to the most favorable areas for tortoises and as a result most of our work occurred in the best currently available habitat. Thus, we may provide overly optimistic estimates of numbers remaining.

The rarity of the Bolson tortoise is evident in the results of our field survey (Table 1). Only about 37% of the transects had any tortoise sign despite our "high-grading" of sites (selection of the most favorable areas based on habitat, isolation from people, and recommendations from local people). Still, we found only 0.17 active burrows/ha ($=17.1/\text{km}^2$), and 0.47 total sign/ha ($=46.5/\text{km}^2$). These figures are much lower than what we found during a training session at the Mapimi Reserve (Fig. 8): 3.5 active burrows/ha ($=350/\text{km}^2$) and 7.0 total sign/ha.

During our surveys, we found only one live tortoise active in the wild and one in a burrow (Table 1). A few more tortoises were detected during study of plots or when we were directed to an active burrow by local residents. However, we observed less than one tortoise for each person-month in the field. These records provide further testimony to the spotty distribution and low abundance of the Bolson tortoise.

The species occurs in only a fraction of its former, larger range due to natural events. The Bolson tortoise is now rapidly losing ground within its last bastion of isolation, the Bolson de Mapimi, because of human depredation and habitat loss.

The Bolson tortoise is on the United States Endangered Species List as well as the Convention on International Trade in Endangered Species (CITES), which means that importation into signatory countries is illegal. Presently, Mexico can punish collection of tortoises with a fine of up to U.S.\$1000. Of equal importance, there is an active effort by Mexico's Institute of Ecology and wildlife department to protect the species. They are coordinating protection of tortoises on ranches and educating their people about the plight of the tortoise. These are encouraging signals for the continued existence of the Bolson tortoise, but protected reserves need to be permanently established.

PART II. ECOLOGICAL DISTRIBUTION OF THE BOLSON TORTOISE

SUSAN S. LIEBERMAN¹

DAVID J. MORAFKA

INTRODUCTION

As extant Bolson tortoise distribution conforms to a simple geographical pattern, a similarly obvious pattern of ecological distribution might be predicted. Indeed, prior literature (previously cited) with its emphasis on the tortoise-tobosa association invited such a prediction. Here we have attempted to test this hypothesis quantitatively. We compare a set of sites, including extralimital sites, by a standard set of environmental parameters. If distribution follows a classical vegetational-climatic-substrate system of associations, we should be able to sequester neat clusters of sites sharing many ecological attributes in common, including relative tortoise presence and density. However, if extirpation (based on opportunities for human predation) is the prevailing limiting factor, the predicted no/low/high tortoise density based clustering of sites will not be manifest. Instead, sites of different tortoise densities may cluster together on the basis of similarities independent of tortoise densities which are determined more by human activities, less by the natural limiting factors.

METHODS

Ecological analyses were tested on a data matrix (Table 4, 5), comparing 35 geographical sites (Table 5) with *G. flavomarginatus* plus several extralimital locales, and one *G. agassizii* locality. Also, three *G. flavomarginatus* sites were subdivided into stations that transected the downslope profile of an alluvial fan or bajada. These three consisted of six to eight sample points on a slope transect, separated by 100-m intervals, which added 22 sites and expanded station observations to 57.

For each of the 35 sites, 33 habitat variables of three types were recorded (Table 4): human impact parameters (variables B-G), vegetation and aspect parameters (I-K), and soil parameters (L-Q). Extirpation (B) was 0 (no) or 1 (yes); goats, cattle, other livestock, roads and human predation (C-E) were 0 (absent), 1 (present) and 2 (dense); human habitat modification (F) was 0 (none), 1 (fenced ranching), 2 (candelilla or guayule gathering), 3 (light farming) and 4 (intense irrigation, with fertilizer and pesticide use); human habitation (G) was 0 (none), 1 (single family), 2 (rancho or ejido), 3 (village), and 4 (town with more than 1000 residents); slope (I) was 0 (0 to ½%), 1 (½ to 1%), 2 (1 to 2%), and 3 (more than 2%); vegetational aspect (J) was 0 (open soil), 1 (patchy grassland, soil 50%), 2 (solid tobosa grass, *Hilaria mutica*), 3 (mixed grasses), 4 (grasses and small shrubs and succulents), 5 (at least 50% large grasses over 1 m in height), and 6 (shrubs and succulents predominant); plant species (K) were 0 (absent), 1 (present), 2 (abundant, at least 25% of the total cover), and 3 (dominant, 50% or more of the total cover); flooding (L) was 0 (no signs), 1 (rare, less than annual), 2 (annual), 3 (multiple within the year); surface type (N) was 0 (outcrop), 1 (pavement), 2 (rock and gravel), 3 (compact sand), 4 (loose dune sand), and 5 (mud). The soil parameters, organic matter, gravel, sand, silt and clay (M1-M5) were recorded as percentiles of the total. Soil particle size (determined by hydrometer) was provided by Babcock and Sons, Inc., Riverside, California. Calcium, sodium, nitrate, and pH (O-R) are measured in real numbers, measured by the same service.

¹ Humane Society of the United States, 2100 L Street, NW, Washington, DC 20037.

Table 4.—Mean, minimum and maximum observed values for each habitat variable, according to the three levels of *Gopherus flavomarginatus* density. Density levels: 0 = absent; 1 = present but rare; 2 = abundant.

Variable	Density = 0			Density = 1			Density = 2		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
B: Extirpation	0.33	0	1	0.04	0	1	0	0	0
C1: Goats	0.89	0	2	1.00	0	2	0.27	0	1
C2: Cattle	1.34	0	2	1.50	1	2	1.73	1	2
C3: Other livestock	1.06	0	2	1.00	0	2	0.91	0	1
D: Roads	1.72	1	2	1.54	0	2	1.73	1	2
E: Human predation	1.39	0	2	1.64	0	2	1.45	1	2
F: Modification	1.50	0	3	1.82	0	3	1.45	1	2
G: Human habitation	1.89	0	4	1.50	0	3	1.82	1	3
I: Slope	0.78	0	3	0.29	0	2	0.64	0	2
J: Veg. aspect	4.20	1	6	4.04	1	5	3.23	1	5
K1: <i>Larrea</i>	2.61	1	3	2.64	1	3	2.91	2	3
K2: <i>Prosopis</i>	1.83	0	3	2.36	1	3	2.00	1	3
K3: <i>Flourensia</i>	1.78	0	2	1.93	1	2	1.82	1	2
K4: <i>Parthenium</i>	1.61	0	3	1.79	1	2	1.82	1	2
K5: <i>Opuntia</i> (pl.)	1.28	0	2	1.39	1	2	1.27	1	2
K6: <i>Opuntia</i> (cy.)	1.44	1	2	1.21	1	2	1.09	1	3
K7: <i>Suaeda</i>	0	0	0	0.11	0	3	0	0	0
K8: <i>Hilaria</i>	2.33	0	3	2.96	2	3	2.64	1	3
K9: <i>Sida</i>	0.89	0	2	1.25	0	2	1.45	1	3
K10: <i>Bouteloua</i>	1.28	0	2	1.52	1	2	1.55	1	2
K11: <i>Sporobolus</i>	1.17	0	2	1.36	1	2	1.36	1	2
K12: Other grasses	1.39	1	2	1.21	1	2	1.45	1	2
L: Flooding	1.39	0	3	1.68	0	3	1.55	0	3
M1: Organic matter	1.36	0.3	3	1.51	0.4	0.7	1.40	0.3	2.8
M2: Gravel	13.80	2	44	8.75	3	23	9.62	0	22
M3: Sand	41.62	15	70	55.00	40	79	48.62	38	72
M4: Silt	35.88	11	59	28.00	10	43	31.69	21	45
M5: Clay	10.02	2	19	8.75	6	14	10.48	7	13.8
N: Surface	2.82	0	5	2.85	2	4	3.33	3	5
O: Calcium	78.40	28	181	110.71	52	95	176.33	41	440
P: Sodium	28.20	5	111	33.00	6	106	70.00	10	190
Q: Nitrate	6.06	1	14.3	10.75	1	20	7.00	3	13
R: pH	7.27	7.1	7.4	7.23	7.2	7.3	7.20	7.1	7.3

These variables were analyzed using SAS (Statistical Analysis System) and EAP (Ecological Analysis Package; written by Dr. Robert Smith, Ecological Data Analysis) on the IBM 3041 computer at the University of Southern California. Univariate analysis included means and ranges for each habitat variable (grouped by tortoise density), and Spearman non-parametric correlations between habitat variables (Fig. 12). In addition, two-dimensional histograms of soil variables and three-dimensional histograms for meristic variables were constructed. All graphics were done using the SASGRAPH procedure of SAS. Multivariate analyses involved the computation of a site distance matrix and a dendrogram that classifies the sites, based on the distance matrix. The dendrogram of sites (Fig. 18) is the product of an agglomerative hierarchical polythetic cluster analysis (using EAP), and was generated using a flexible sorting strategy on a distance matrix. The index chosen to generate the distance matrix was the Canberra-Metric index (Clifford and Stephenson, 1975).

RESULTS

We compiled an ecological data base for *G. flavomarginatus* (Table 4 and 5) by quantifying site conditions for several key parameters, the range of environmental conditions at known tortoise populations, and the degree of overall similarity shared by the sites.

Table 5.—*Gopherus flavomarginatus* habitats studied: site numbers and localities. Asterisk (*) denotes that 8 transects were taken at each of these sites, making a total of 57 observations.

District 1: Coahuila, Americanos	
1	Rancho El Socorro
2	Laguna del Coyote
3	Americanos
4	Rancho La Mena
5	El Matrimonio Viejo to Rancho Berrinche
6	South of El Matrimonio Viejo
District 2: Chihuahua, Sierra del Diablo	
7	Rancho La Ventura
8*	Cerros Emilio
9	Rancho Benthon
10*	Rancho Peñoles and foothills
11	Rancho Las Esperanzas
12	Rancho Arenal
13	Guimbalet
14	Rancho Robles
15	Rancho Cerros Blancos
District 3: Chihuahua, Durango	
16	Rancho Diana and Rancho Tepetate
17	Rancho San Isidro
18	Hills West, SW of Yermo
District 5: Coahuila, Mapimi Core	
19	Rancho Las Lilas
20	Rancho Santa Maria
21	Rancho El Cinco
22	Carrillo
23	Ejido La Soledad
24	South, SW of Mercurio
25	Rancho La Flor
26	East of Ceballos
27	East of Sierra Banderas
28*	Rancho Aguaje San Ignacio
29	Vicinity of Yermo
30	South, SW of Las Lilas
31	Lomas de Canelo
32	South of Cerro San Ignacio
District 6: Chihuahua, Sierra Los Remedios	
33	Ejido Division del Norte
34	Rancho San Miguel
35	Rancho Alejandro Carrillo
District 7: Extralimital; Coahuila	
36	Rancho Dahlia
District 8: Extralimital; San Bernardino County	
37	Kelso

Relationships Between Habitat Variables

A maximum of 33 variables (Table 4) were measured at 35 sites (Table 5). Three of the sites were compound stations, as noted in Methods.

There was a series of both positive and negative correlations between habitat variables and tortoise densities (Fig. 13–17). Increasing densities of goats, other

SPEARMAN NON-PARAMETRIC CORRELATIONS

A B C1 C2 C3 D E F G I J K1 K2 K3 K4 K5 K6



Fig. 12.—Spearman non-parametric correlations between environmental variables encoded in Table 4. A black rectangle indicates a statistically significant correlation between the intersecting variables.

livestock (except cattle), and *Opuntia bradtiana* cactus all correlate negatively with tortoise densities. Cattle, increasing calcium and sodium concentrations in the soil, and densities of creosote (*Larrea divaricata*), tobosa grass (*Hilaria mutica*), *Sida leprosa*, grama grass (*Bouteloua ramosa*), and dropseed grass (*Sporobolus airoides*) all correlate positively with tortoises. Intermediate values of gravel and sand were most frequently associated with higher densities of tortoises.

However, using Spearman non-parametric correlation coefficients, few of these correlations are statistically significant. Extirpation (obviously) and calcium soil concentrations correlate significantly with tortoise densities. Even the calcium figures are suspect, since some samples were taken in or near disturbed nest sites where the soil contained scattered egg shell fragments.

Many significant correlations exist between habitat variables measured (Fig. 12). Suites of significantly correlated variables often form naturally related groups. For example, human habitation (G) correlates positively with all livestock, roads, human predation, and habitat modification (agriculture). Several of the floral factors also cluster in a positive correlation group. Item "K 12" (other grasses) correlates positively with goats, human predation, human habitat modification, slope, the shrub mariola, *Parthenium incanum*, and the grasses *Hilaria mutica* and *Sporobolus airoides*. Flooding (item L) similarly correlates with livestock, slope, vegetational aspect, specific floral taxa such as *Prosopis glandulosa*, *Opuntia leptocaulis*, *Parthenium incanum*, *Hilaria mutica*, *Sida leprosa* and surface texture (N). These sets of parameters are probably linked, reflecting interrelationships among slope, drainage, human land-use, vegetation and, to a lesser extent, soil structure.

The preceding correlations establish two major characteristics of tortoise habitats: (1) tortoise densities and range limits are not predicted significantly by any single environmental parameter, and (2) many of the environmental parameters selected to compare sites are not independent variables, but rather expressions of underlying causal agents such as topographical relief (drainage) and human presence. Even these fundamental agents are not entirely independent. Also, environmental parameters tend to become less variable when associated with higher tortoise densities (Table 4).

Single Habitat Variables Correlated with Tortoise Densities

Although no single factor (meristic parameter) correlated significantly with tortoise densities, several descriptive patterns did characterize known tortoise sites. We organized variables into three groups: substrate, flora, and human impact. An obvious fourth category, climate, was omitted because site specific data is almost non-existent, and because long-term data available from adjacent ranch and village stations indicate little difference between sites. Summaries of available climatic data have been presented elsewhere (Cornet, 1984; Morafka, 1982; Morafka et al., 1981; Schmidt, 1979, 1986; Tamayo, 1962). The regional climate has been classified as warm temperate to subtropical with Schmidt and Cornet emphasizing the latter.

Substrate

Surface soil samples were compared for percentage content of sand, clay, silt, and organic matter (Fig. 13). The percentages of mean conditions for these variables in substrates at high density tortoise sites (Table 4) were: gravel, 9.6% (range

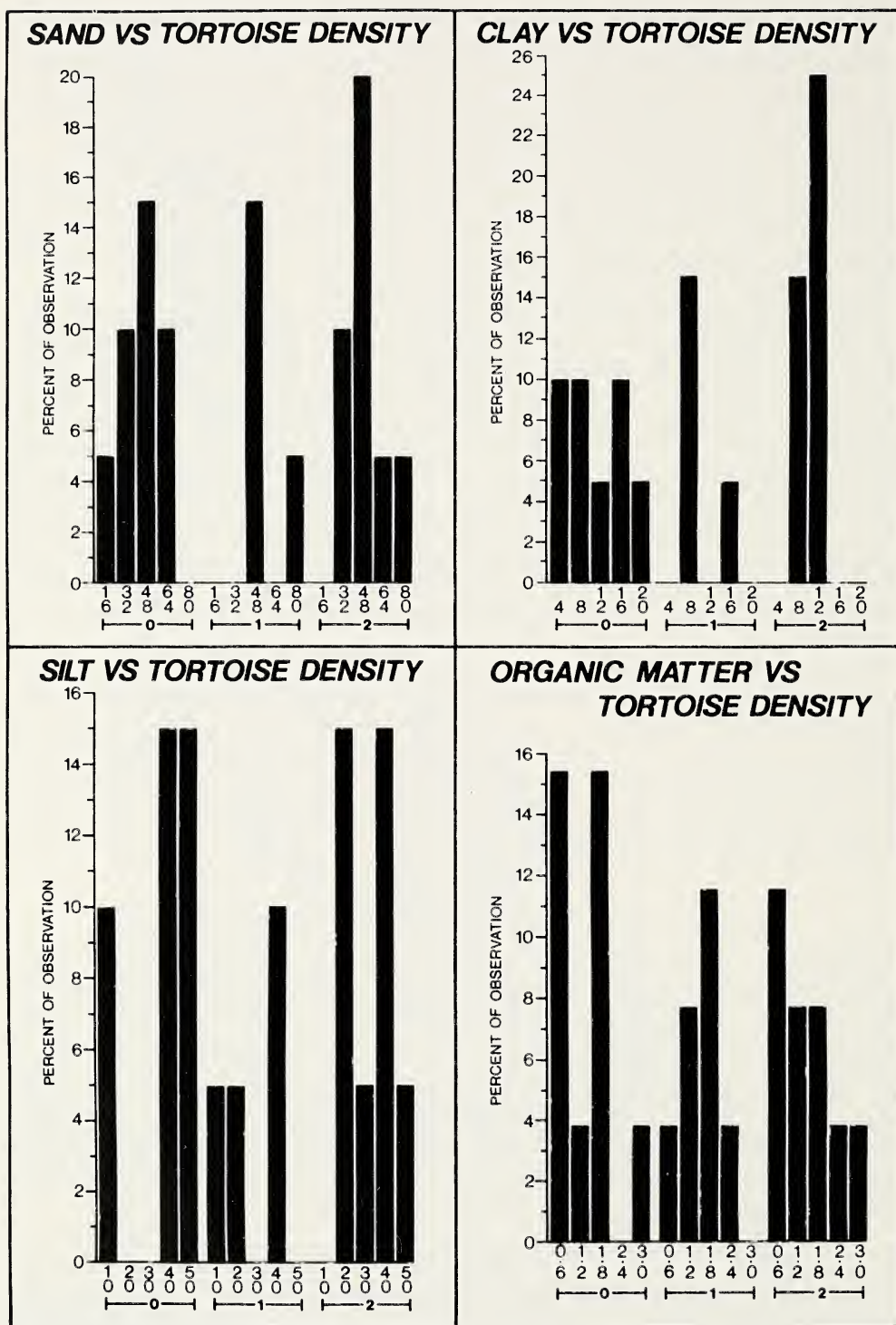


Fig. 13.—Histograms of substrate characteristics at localities with different densities of *Gopherus flavomarginatus*.

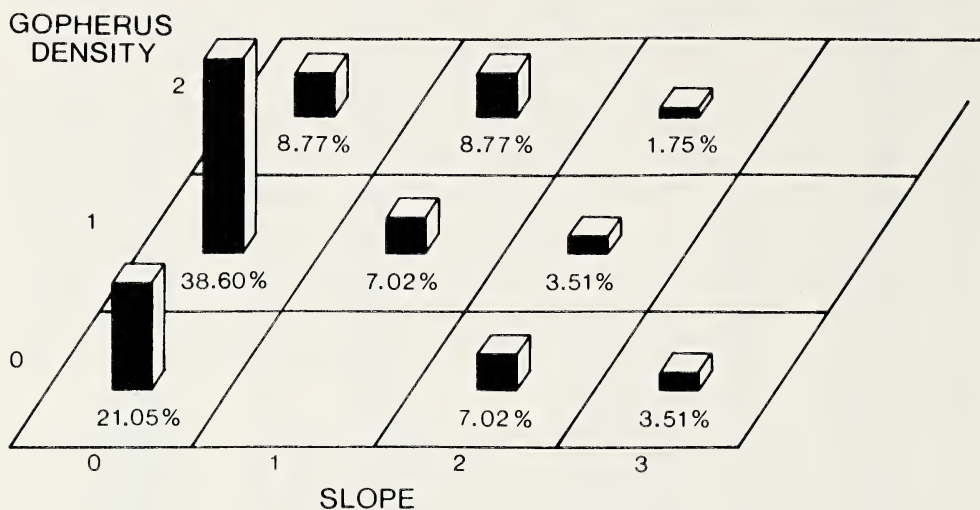
3–23%); sand, 48.6% (38–79%); silt, 31.7% (10–45%); and clay, 10.5% (6–14%). Tortoise presence and/or high densities are most frequently associated with sites composed of intermediate grain sizes (Fig. 13). Such soils are considered loams (or sandy loams). Presumably, the typical values reflect the intermediate placement of most burrows, just slightly above the playa floors of closed basins. Exposure to flooding once or twice each year apparently does not eliminate tortoises. Individuals at the Mapimi reserve have been observed swimming into and out of flooded burrows (G. Aguirre, personal communication). Burrow floors usually dip upward about one meter before their termination, inclining toward a final chamber which could trap a reservoir of air if flooded. Thus, based both on observation and burrow structure, five to ten-day intervals of local flooding may not drown tortoises. Temporary burrow inundation is also a common phenomenon in the related *G. polyphemus* (Means, 1982). In contrast, seasonal bodies of standing water, such as on flooded playas, do appear to exclude tortoises. Even when bolson floors are covered with dense uniform stands of tobosa grass (*Hilaria mutica*), a staple of tortoise diet, burrows are generally absent where there is as previously noted a history of seasonal flooding.

At the other extreme, tortoises are absent from the uppermost parts of slopes (Fig. 14) where the incline is in excess of 2.5° or 3°, or when substrates are rock outcrop or consist of more than 25% gravel. However, *G. flavomarginatus* burrows were found subducting the edge of desert pavement. Unlike other *Gopherus* this species apparently does not use rock overhangs or shallow pallets as cover where substrate hardness precludes deeper excavation (Luckenbach, 1982; Auffenberg and Franz, 1982). Areas with intermediate soil grain sizes, drainage and slope appear to have the most tortoise burrows. Ultsch and Anderson (1986) reported that tight, clayey soils engendered potentially stressful hypercarbia in *G. polyphemus* burrows. Such stress may explain the correlation between shorter burrow length and tight soils in Georgia. Similarly, very compact soils in bolson floors, high in clay content, may operate as density independent limiting factors on *G. flavomarginatus* distribution, even at sites where tobosa grasslands are particularly dense and productive.

While extremes in slope, substrate, and flooding may be local limiting factors, their role in determining the overall limits of tortoise distribution is less clear. Extensive regions of limestone uplifts, like the sierras Almagre, Mojada and Diablo, limit and disrupt tortoise distribution in the northwestern portion of its range. Sampling from this region indicates that more than just substrate is involved. Specifically, soil values for extralimital Rancho Dahlia (Chihuahua) are within the values for sites inhabited by the tortoise. Only a weakly inclined (2–3°) gravel ridge separates the Dahlia area from high density populations of the adjacent Rancho Ventura to its west (District #2).

Comparative soil values typical of *Gopherus agassizii* habitat (an extralimital site) were taken at Kelso, 35 km south of Baker on the Kelbaker Road, San Bernardino County, California. The site is dominated by creosote bush scrub and Joshua tree desert scrub. Soils have gravel content values about 400% greater, and silt levels about 50–65% lower than soils usually utilized by *G. flavomarginatus*. According to Luckenbach (1982), such light gravel-clay soils typify *G. agassizii* habitats in the Mojave Desert of California, but they may range from heavy gravels to sandy loams. In contrast, *G. flavomarginatus* appears to be largely restricted to loam/sandy loam soils of the desert Sierozem of Aridosol classification groups.

SLOPE VS TORTOISE DENSITIES



FLOODING VS TORTOISE DENSITIES

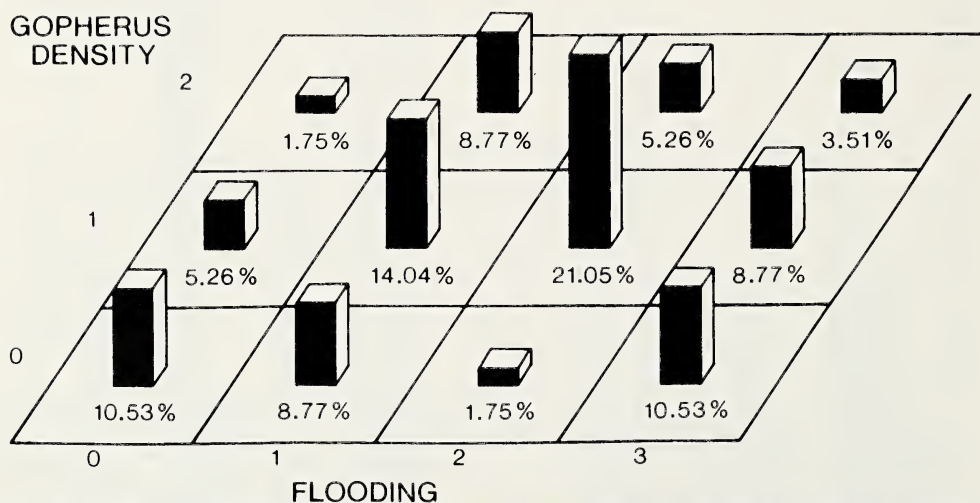


Fig. 14.—Histograms of topographic characteristics at localities with different densities of *Gopherus flavomarginatus*.

Flora-Vegetation

The percentages of sites with various combinations of tortoise and plant species densities are shown in Figures 15 and 16. Axis values are the same meristic measures of tortoise density as used in Table 4. The five plant species were chosen as representative of: a major food species (tobosa), high frequency dominant (tobosa grass and creosote bush), subdominants (mariola and tarbush), and an edaphic indicator of increased (subsurface) water availability (*Prosopis glandulosa*).

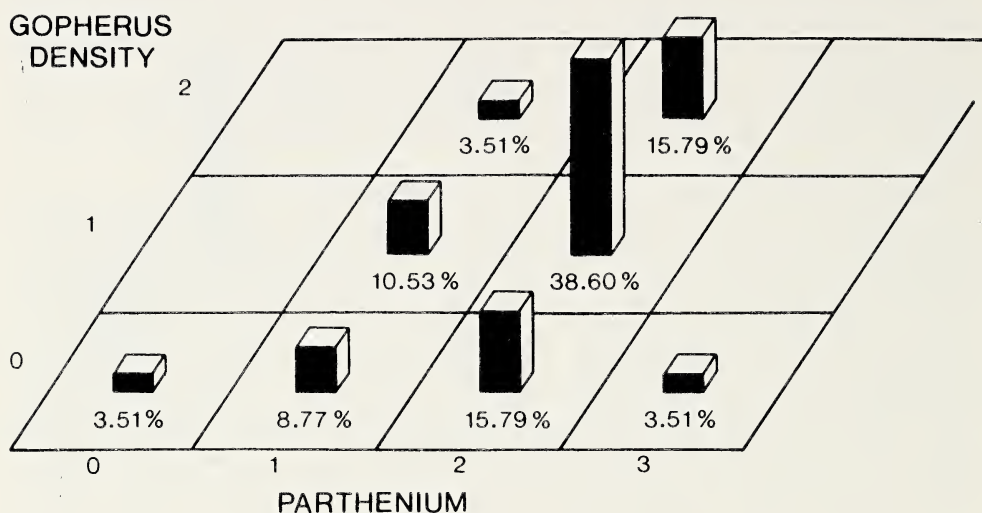
Tobosa grasslands (Henrickson and Johnston, 1986) occurred in almost all categories. Densities of tobosa and tortoises also have a positive (though not statistically significant) correlation. Sites devoid of this grass are generally not occupied by the tortoise (Fig. 15). However, our field observations do not indicate tortoise dependence on, or exclusive correlation with tobosa. For example, the marginally extralimital site at Rancho Dahlia (Bolson de Lipanes) has large tobosa grasslands, but no tortoises. Such grasslands continue both north and south of the Mapimi region, from southeast Arizona and Texas to Zacatecas (Morafka, 1978; Van Devender, personal communication, 1987; Lowe, 1964). Yet these regions, including the immense Llano del Guaje, a plain immediately northeast of tortoise populations at Rancho El Socorro in Coahuila, presently lack tortoises. This plain has dense, uniform carpets of tobosa but relatively few other species of vascular plants. Such conditions are often associated with saline clayey soils and/or repeated flooding. Furthermore, even within the known range of the tortoise, nuclear colonies most often occur in stands of mixed grasses interspersed with open flats and varied shrubs, above or peripheral to continuous tobosa matting (Morafka, 1982).

The apparent ecogeographical relationship between tobosa and *G. flavomarginatus* is probably largely due to coincidental contemporary climatic and substrate requirements that make possible the largely syntopic distribution. Dietary importance of tobosa to tortoises is probably reflective of availability, not preference or coevolution. Aguirre (personal communication, 1986) confirms the significant role of other grasses in tortoise diet. Van Devender (personal communication, 1987) concluded the tortoise occupied tobosa-free communities during late Wisconsin glacial times in Big Bend, Texas.

The creosote bush is a dominant and widespread plant at Chihuahuan Desert localities both within and external to the tortoises' range. The most common association (33% of total sites), was creosote and intermediate densities of tortoises. Few tortoise sites were devoid of creosote. However, tortoise colonies occur in flood plains covered by the halophytic shrub *Suaeda* and tobosa near Arroyo Vega at Rancho La Flor (near Laboratorio del Desierto), Durango, where there is a local absence of creosote.

Tarbush (*Flourensia cernua*) and mariola (*Parthenium incanum*) are subdominant shrubs endemic to the Chihuahuan Desert (Henrickson and Johnston, 1986), and often occur in areas of tortoise populations, although in reduced abundance relative to creosote (*Larrea divaricata*) (Fig. 15, 16). Mesquite species (typically *Prosopis glandulosa*) are also ubiquitous shrub components of the Chihuahuan Desert, and may be a dominant or subdominant plant depending on the depth of the local water table and surface relief. At many tortoise sites, 37% mesquite was the subdominant plant.

PARTHENIUM VS TORTOISE DENSITIES



HILARIA VS TORTOISE DENSITIES

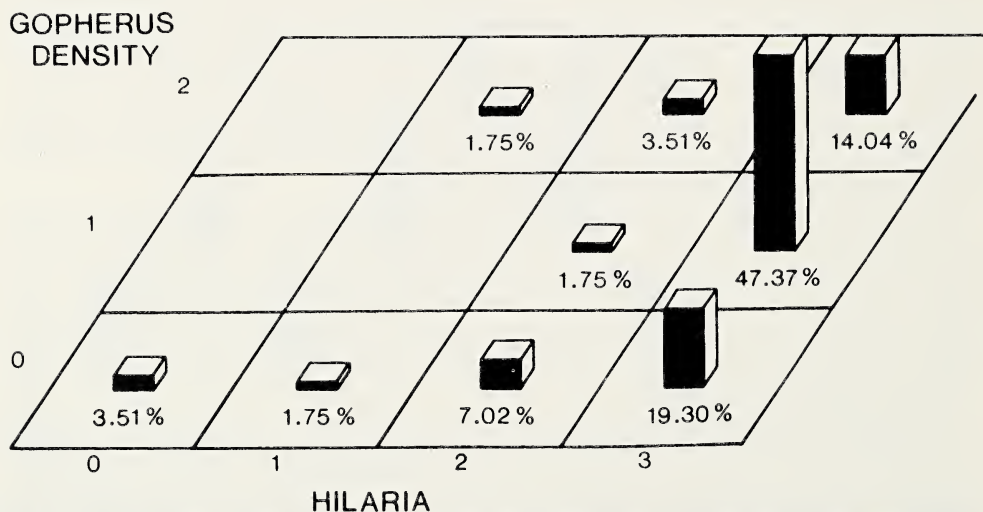


Fig. 15.—Histograms of densities of the shrub mariola (*Parthenium incanum*) and tobosa grass (*Hilaria mutica*) at localities with different densities of *Gopherus flavomarginatus*.

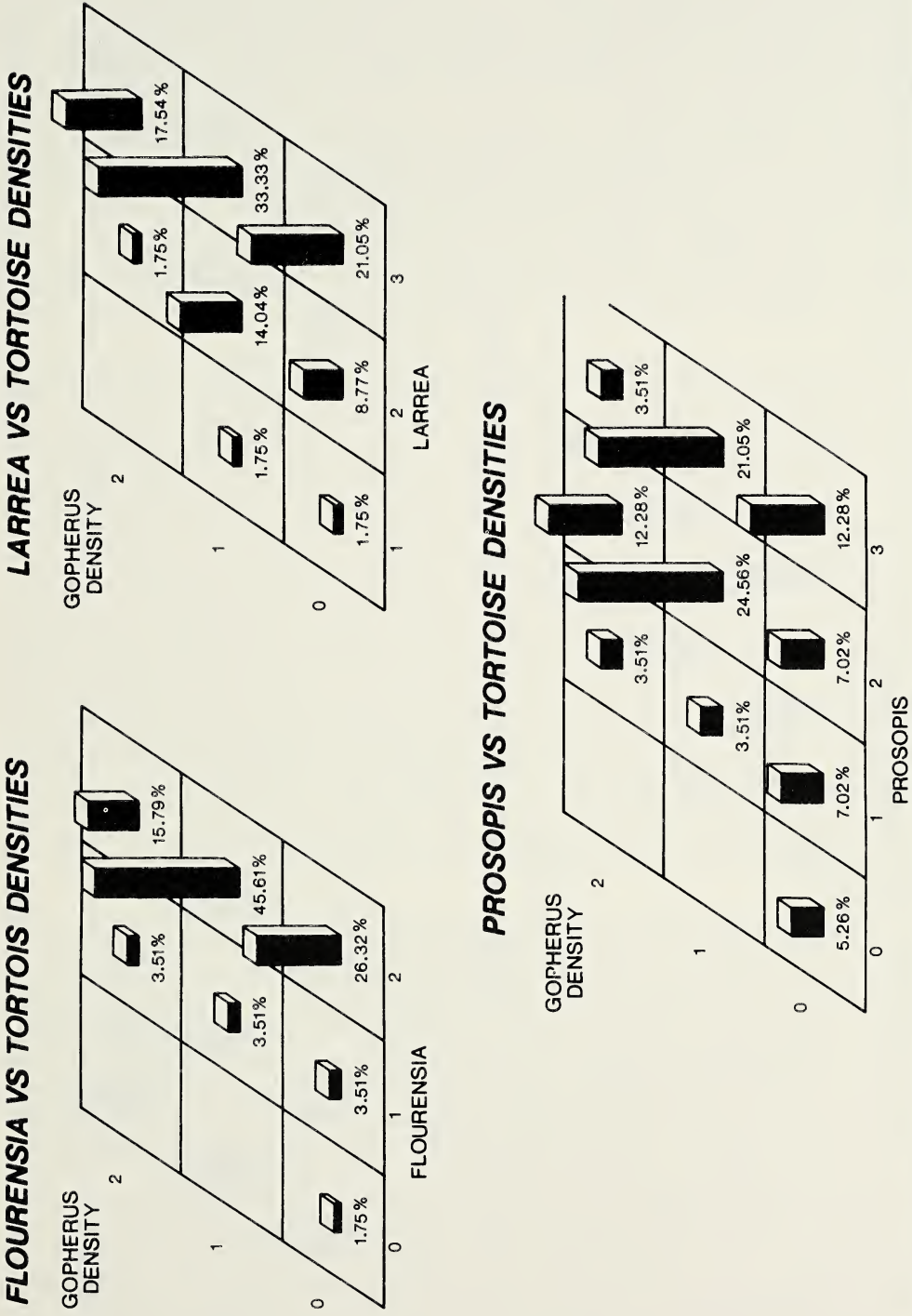


Fig. 16.—Histograms of densities of tarbush (*Flourensia cernua*), Creosote (*Larrea divaricata*), and mesquite (*Prosopis* sp.) at localities with different densities of *Gopherus flavonarginatus*.

Human Impact

Human activity influences many environmental factors (Table 2). For example, we selected three representative variables for characterization of sites (Fig. 17): human predation as an indicator of direct intervention; goats as a measure of agricultural and livestock disturbance; and roads as a gauge of indirect physical environmental disturbance.

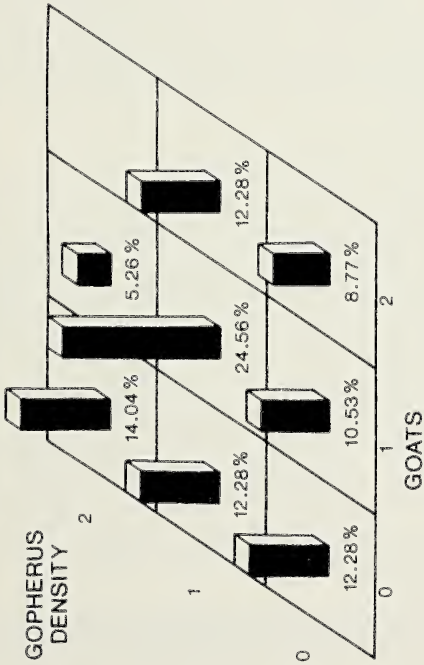
Human predation occurs at virtually all sites (93%). Even sites now lacking tortoises were scored positively for predation because towns like Carillo, Ceballos, and Escalon are within zones where tortoises were recently extirpated. These towns still serve as "staging" areas for forays of tortoise hunters.

All of these tortoise localities have been subject to moderate (48%) or intense (52%) human predation. Only the MAB Mapimi Reserve near Rancho San Ignacio is now excluded. Even so, these tortoises have received protection only since 1980.

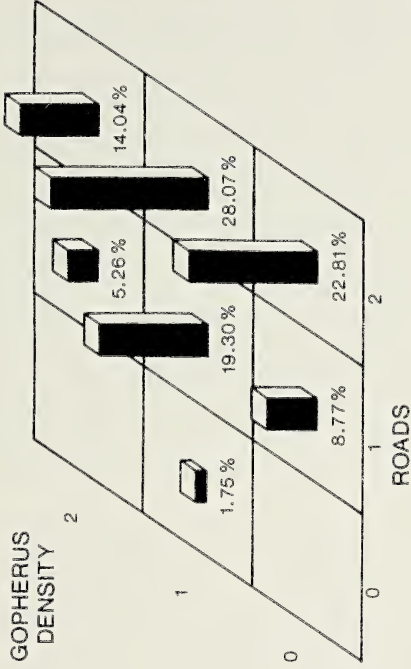
Goat density varies inversely with tortoise density. At 26% of all sites, tortoises were present or abundant when goats were absent. In contrast, 18% of all sites were inhabited only by goats. No areas with high-density goat populations also had high-density tortoise populations. Part of this inverse correlation may be due to a preference by goats for rocky substrates especially for prolonged browsing. However, livestock have been implicated as competitors for forage with the Desert tortoise, *Gopherus agassizii* (Woodbury and Hardy, 1948; Bury and Marlow, 1973; Coombs, 1979; Berry, 1978). It is known that sheep, in particular, may outcompete tortoises for the same plant species. It is uncertain if goats are equally influential as competitors, since they browse on a wider variety of vegetation. The presence of goats may have a secondary impact, as they generally are herded near villages or ejidos, where numerous goat herders may prey on tortoises. In contrast, in the Chihuahuan Desert cattle are more numerous than goats and have a major local impact on density and diversity of grasses (Enriques, personal communication). Cattle, by virtue of their greater weight, introduce the additional danger of simply crushing hatchling and juvenile tortoises under foot. Yet this study establishes no discernible relationship between cattle and tortoises (Fig. 17), perhaps because cattle are less intensive grazers than goats. Cattle in the Chihuahuan Desert are restricted to the vicinity of waterholes much of the year, and are not tended by herdsmen.

Goats and cattle reduce available protein-rich forage (new shoots, flowers, and seeds) which may be critical to hatchling tortoise nutrition. The importance of high protein diets for *G. flavomarginatus* was studied 28–30 August 1983. Fecal samples were collected from both adult and juvenile tortoises at the MAB Mapimi Reserve and from a captive colony at Audubon Research Ranch in southeast Arizona. Hatchlings typically selected plant species and parts yielding twice the protein (16%) of that ingested by adult tortoises (8%) (Adest et al., in press). Such high protein diets probably contribute significantly to hatchling survivorship and growth. If so, selective competitors such as livestock might adversely affect protein resources available to tortoise hatchlings, the most vulnerable class in the population. Overgrazing may have the more subtle effect of skewing tortoise sex ratios in favor of females. The primary study population at Mapimi (Adest et al., in press) shows a 3:1 female to male ratio. Higher soil surface temperatures result from overgrazing, producing higher incubation temperatures. In emydid/testudinid chelonians this determines a higher proportion of females. Bull (1980) has suggested that habitat disturbance (such as floods clearing vegetation) may induce

GOATS VS TORTOISE DENSITIES



ROADS VS TORTOISE DENSITIES



HUMAN PREDATION VS TORTOISE DENSITIES

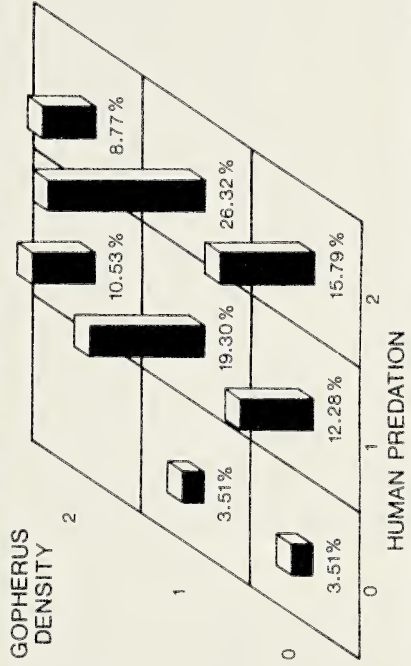


Fig. 17.—Histograms of measurements of human impact (goats, roads, direct predation) at localities with different densities of *Gopherus flavomarginatus*.

the higher temperatures and ratios. Recent climatic perturbations may also have contributed to the last 500 years constituting a relatively warm episode (Van Devender, personal communication, 1987). Controlled comparisons may eventually reveal overgrazing to be a mode of "thermal load" resulting in sex class imbalances demographically. Jarchow (personal communication, 1987) has sexually diagnosed 40 adults at the much less grazing-dense grassland of Cerros Emilio, Chihuahua. He reports a sex ratio skewed moderately toward males.

Bjorndal (1982) has described repetitive grazing along the same trails by the Green sea turtle, *Chelonia mydas*, and suggested that such behavior stimulated and harvested new shoot growth, higher in protein. The Gopher tortoise, *G. polyphemus*, mostly forages within 30 m of its burrow and some individuals forage along meandering paths (McRae et al., 1981). Identical behavior occurs in *G. flavomarginatus* (Morafka, 1982; Aguirre et al., 1984). This species follows regular routes to both food and alternative burrows, with males maintaining larger home ranges inscribed by such pathways. Even patchy, episodic overgrazing by livestock might disrupt these routes and diminish their nutritional yields, which are often traveled with rigid repetition by the tortoises.

There is a positive association between road development and tortoise concentrations (Fig. 17). Almost all localities (99.25%) were accessible by roads or within 1 km of a road. Few tortoise localities are known in areas where roads are absent. All three colonies we studied were within 0.5 km of a road. Selection of sample sites may be biased in favor of disturbed, accessible areas, since we usually were guided to already discovered and therefore disturbed tortoise localities by local residents, who utilize the "neighborhood ranch to market" roads. Thus, our sample sites are mostly confined to already discovered and therefore disturbed settings. However, many of these "roads" are dirt paths meandering through the desert, and others are recent natural gas exploration roads which crisscross almost every basin at about 5 km intervals (and in straight lines). The older road system is sometimes obliterated or confused by the PEMEX roads, because local people soon use the newer access routes. Also, the older roads tend to be at mid-elevations above the playas (flooded areas) and below the rugged limestone ridges; thus the roads often traverse prime tortoise habitat.

Multivariate Analysis: Classification of Sites

We classified sites examined into a hierarchical dendrogram based on the Canberra-Metric distance index (Fig. 18). Given the complexity of clusters generated, there are few unifying or causal factors that might explain the cluster organization. In a few cases, similarities in slope and drainage combine sites that share a similar soil structure and vegetational cover. The bottom cluster of the dendrogram (from 28-8 to 8-1) includes a number of substations within transects (as indicated by the hyphenated numbers). Since these transects were run down-slope along well drained bajadas, they may exhibit similarity based on this shared topography. Site 37 (extralimital gravel-Joshua tree), representing the Desert tortoise *Gopherus agassizii* is clearly distinct from all sites for *G. flavomarginatus*, confirming that habitat differences separate *G. agassizii* from the "true" *Gopherus* described by Bramble (1982). Were the desert tortoise locality from the Sonoran Desert of Arizona where rocky substrates are frequented, the differences might have been even greater.

The dendrogram clusters show little other internal continuity. All but one of the five major clusters include sites in which tortoises are absent, present, and

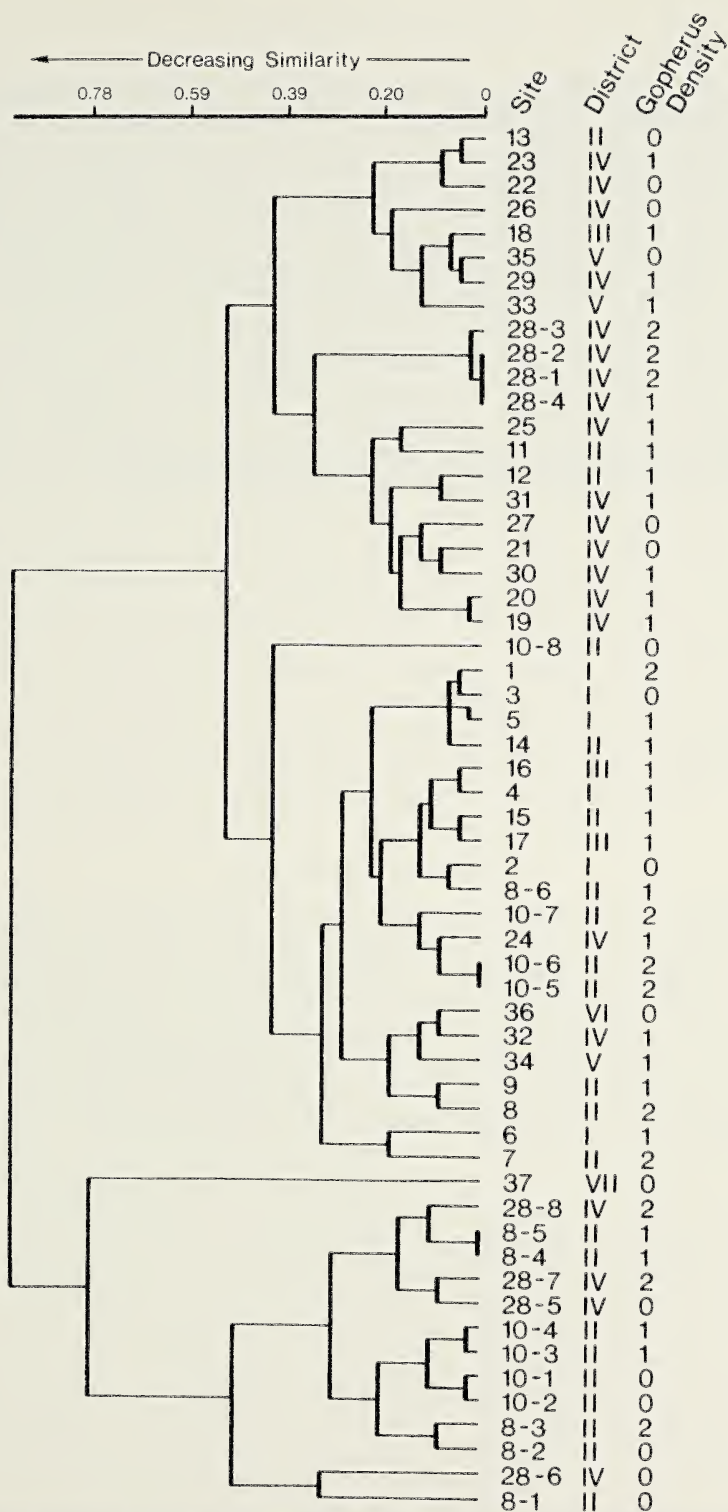


Fig. 18.—Dendrogram of similarity classifying sites listed in Table 5 in terms of the environmental parameters encoded in Table 4.

dense. Clusters show affinities based upon geographical district. The bottom cluster is composed predominantly of District #2 (Sierra del Diablo) sites, but geography is far from an absolute influence. The tight clustering of Rancho La Ventura (8-5) with the MAB Mapimi Reserve (28-8) brings together a northernmost site with one from the south. Perhaps most striking among closely linked sites is the pairing of the northern extralimital Rancho Dahlia (36) with our primary tortoise study population at Cerro San Ignacio (32). As noted in earlier floral analyses, there appears to be little differentiation between extralimital and inhabited localities. The local distribution of *G. flavomarginatus* does not seem associated with any of the recorded environmental factors, either taken alone (such as tobosa, *Hilaria mutica*) or in the multivariate combinations represented by distance indices. The present fragmented occurrence due to human predation may obscure many other relationships. Therefore, historical biogeography may serve better to resolve current tortoise distributions, both ecological and geographical.

PART III. HISTORICAL BIOGEOGRAPHY OF THE BOLSON TORTOISE

DAVID J. MORAFKA

INTRODUCTION

How Bolson tortoise populations came to exist only in the Mapimi bolsons and why they are now confined here remains unanswered. Since related tortoises in the genera *Stylomys* and *Gopherus* have the most complete fossil record of any extant North American reptile group (Auffenberg, 1971, 1976; Auffenberg and Franz, 1982; Brattstrom, 1961; Messing, 1986), paleontological evidence may yield insights into their evolution and biogeography. While even this substantial record does not provide unambiguous indications of generic (or species group) divergences, or species origins, its closing chapters, the late Wisconsin and Holocene epochs, do provide a detailed and sequential paleoecology for the northern Chihuahuan Desert region. That sequence provides us with an unusually good opportunity to evaluate competing hypotheses about the demise of North America's megafauna, using the declining population of our largest surviving "temperate" terrestrial reptile, the Bolson tortoise, as a test case.

THE TERTIARY PERIOD

Late Tertiary environmental changes, especially the repeat orogenies of the Miocene Epoch, may have induced differentiation of the more specialized and fossorial *Gopherus* from a generalized *Xerobates* stock. Bramble (1982) assembled a transformational series of characteristics from head (especially inner ear), neck and forelimb morphology that demonstrated the more fossorial specialization of true "*Gopherus*," its differentiation from the more generalized genus "*Xerobates*" and its special adaptations and historical affinities for semiarid sandy substrates. Others contend that *Xerobates* are not a natural sister group—just primitive *Gopherus*. In light of such criticism, we shall treat *Xerobates* as synonymous with *Gopherus*, employing only the latter term.

Bramble (1982) indicated that the Miocene differentiation of true "*Gopherus*" occurred on the Great Plains and the adjacent emerging Mexican Plateau. Cooling trends, combined with increased aridity and the dilation of seasonal temperature extremes, fostered the development of sandy, well-drained soils. The appearance and proliferation of *Gopherus* was correlated with development of these soils. Axelrod (1950, 1958, 1979; Axelrod and Raven, 1975) also noted the expansion of semiarid vegetation during this same period (originating in late Oligocene and earlier). Morafka (1978) and Van Devender (1986) recognized parallel modernization in the Miocene flora and herpetofauna. During the early Tertiary, a generalized track of semiarid biota began to coalesce into the Madro-Tethyan Geoflora (Axelrod and Raven, 1975). This "track" established an intermittent northeastern American connection with Eurasia and included the now subtropical helodermatid lizards (Hoffstetter, 1957; Stevens et al., 1977).

A second subordinate track of more arid-adapted biota separated from the Madro-Tethyan Geoflora during Mio-Pliocene times. This derivative system involved both sclerophyll and grassland vegetation and may have reached peak aridity (possibly comparable to modern desert conditions) in the early Miocene (Bramble and Hutchinson, 1980; Bramble, 1982; Hutchinson, 1982), late Miocene (Van Devender, 1986) or late Pliocene (Morafka, 1978). The confusion regarding the arid peak chronology stems from the differing empirical bases used, and from a recent revision of the Mio-Pliocene boundary from 11 My to 5.5 My. This latter change placed many formerly Pliocene records within the revised Miocene time (Van Couvering, 1978). This track approximates the Mojavia Geoflora (Axelrod, 1958) in terms of chronology, geography, and ecology.

Southwestern landscapes and climates underwent a second profound modernization. On the Pacific Coast, Baja California emerged (Gastil et al., 1975) while the orogeny of the Coahuila Folded Belt (and the Sierra Madre Oriental) contributed not only to the development of the Mexican Plateau, but also to the recession of the Mississippi Embayment and its associated maritime climates. Orogenic activities in the intervening continental interior accentuated rain shadow effects of the Rocky Mountains upon the Great Plains, and volcanic extrusives contributed significantly to the development of the Sierra Madre Occidental in Mexico (Christiansen and Lipman, 1972; McDowell and Keizer, 1977). Pliocene and early Pleistocene coolings combined with repeated faulting and uplift of existing blocks to separate the modern deserts of North America (Morafka, 1978; Axelrod, 1979).

Tertiary Mojavia was already a temperate, semiarid complex, including thorn scrub, chaparrals and savannas, eventually becoming a desert in the south. These ecosystems were species rich compared to current habitats, and less characterized by single dominants such as the creosote bush (*Larrea divaricata*), which was documented in North America no earlier than 18,000 yr BP. While *Larrea*'s first continental appearance is unknown, its continuous modern occupation of the northern Chihuahuan and Sonoran deserts extends back only some 5000 years (Van Devender et al., 1987). Throughout Mojavia, climates were more mild and more precipitation occurred, even between rainy seasons. The Mojavia landscape was probably an edaphic patchwork of scrub and grasslands grossly similar to current vegetation in the Bolson de Mapimi. The flora and reptile fauna were dominated by extant species or species groups (Morafka, 1978; Van Devender, 1986). From this general region, California to Kansas and south to the Mexican Plateau, the Late Tertiary herpetofauna included modern genera such as the anurans *Bufo* and *Scaphiopus*, the lizards *Gerrhonotus*, *Sauromalus*, *Heloderma*, *Ctenosaura*, *Phrynosoma*, *Crotaphytus*, *Sceloporus*, and possibly *Dipsosaurus*, and the snakes *Nerodia*, *Coluber*, *Heterodon*, *Pituophis*, *Agkistrodon*, *Sistrurus*, and *Crotalus* (Gehlbach, 1965; Auffenberg and Milstead, 1965; Brattstrom, 1955, 1967). The chelonian genera *Terrapene*, *Trionyx*, *Chrysemys*, *Kinosternon*, and *Geochelone* were also represented. The late Tertiary of Mojavia not only included a predominantly modern herpetofauna, but also a shift from browsing to grazing dentition in mammalian herbivores (Stevens et al., 1977; Woodburne et al., 1974). This latter shift was probably a response to the coalescence of patchy, local grassland into major prairies and open woodlands during the Miocene. This transition was paralleled by the shift in jaw morphology (*os transilens* development) associated with the evolution of *Gopherus* from "*Xerobates*" (Bramble, 1971, 1982).

The expanding and increasingly arid communities of Mojavia created an arid

midcontinental track into which diverse species became entrained at different times. Many taxa, including *Gopherus*, probably evolved *in situ* as more arid circumstances overtook them. Farther north, suitable habitats of early Tertiary times in the Great Plains underwent cooling trends, which likely caused the extinction of tortoises (Auffenberg, 1969, 1974).

Bramble (1982) suggested that virtually all Tertiary records for true *Gopherus* were from east of the Continental Divide, while "*Xerobates*" during this time period was from the west. He further suggested that members of the two groups have never been found in the same deposit, even during the late Tertiary Period when true *Gopherus* (Bramble's genus) may have extended west to western Arizona and *G. agassizii* (Bramble's *Xerobates*) occurred east to Texas and New Mexico. Auffenberg (1974) however, reported *G. canyonensis* from the Pliocene (Blancan) of southeastern Arizona. Currently, *Gopherus flavomarginatus* occurs within 150 km of *Gopherus berlandieri* in central Coahuila. If the two genera were once sympatric, different substrate preferences may have segregated the two stocks into microallopatry, producing a pattern of local complementarity. The upland distribution of *Gopherus agassizii* in the eastern Sonoran Desert today may have been reinforced by past coexistence with *Gopherus flavomarginatus*, which seems better adapted to valley floors and margins than does *G. agassizii*. In contrast, historically allopatric *G. agassizii* populations in the Mojave Desert, while topographically widespread, have no particular affinity to upland habitats (Luckenbach, 1982; Jarchow, personal communication).

Two critical biogeographical questions may be addressed in the Tertiary record. First where, and second, when did the speciation of *G. flavomarginatus* occur? While the fossil record reveals an apparent time and setting for the differentiation of the specialized *polyphemus*-*flavomarginatus* group from more generalized antecedents, it yields no such clear pattern for the speciation of *Gopherus flavomarginatus*. Temporally, no unambiguous record for the species exists prior to the late Pliocene Period of West Texas (for the putative conspecific *G. huecoensis*: Auffenberg, 1974, 1976). In this instance, negative data may in fact allow the possibility of a relatively recent history for *Gopherus flavomarginatus*. Late Pliocene fossils from the same region yield *Gopherus pertenuis*, *G. hexagonatus*, *G. laticaudatus*, and *G. canyonensis*. All of these taxa appear to be closer to the extant Florida gopher tortoise *G. polyphemus*, and several may be conspecific with the latter. Meylan (1981) suggested a central Texas-Florida connection between semiarid adapted reptiles (*Crotalus atrox* and *Crotalus adamanteus* being the particular example) was sustained throughout much of the Pleistocene. During late Wisconsin time oak-hickory-southern pine forest dominated the Gulf Coast Plain (Delcourt and Delcourt, 1985). However, during the short, but frequent, interglacials pine parklands may have circumscribed the northern rim of the Gulf of Mexico, reestablishing this track for semiarid reptiles through glaciopluvial intervals. Van Devender (1986) has documented that similar grasslands occurred on the Mexican Plateau and adjacent West Texas. Therefore, the question remains as to how *G. flavomarginatus* separated from a *polyphemus*-like sister species (*Gopherus canyonensis*) to the east. Sympatric speciation is unlikely, especially in light of the extremely conservative karyotypes of chelonians in general and testudinids in particular (Dowler and Bickham, 1982). Assuming allopatric speciation the late Tertiary uplift, possibly Trans-Pecos Texas ranges (the Guadalupe, Davis and Chisos in the Rio Grande Rift of Baldrige et al., 1984), extending southeast through the Coahuila Folded Belt, and terminating in Sierra Madre

Oriental, might have separated the species. This diagonal series of ridges, established earlier in the Tertiary, may have been uplifted sufficiently to isolate *Gopherus flavomarginatus* from its eastern congeners. Geological time estimates would place some of these uplifts approximately two to three million years ago. Early Pleistocene continuation of these uplifts, and parallel orogenic activity in the Saladan region may have reduced its maximum Pliocene range by 30–50%. Confounding this simple scenario is the presence of late Tertiary *G. canyonensis* in Arizona, far to the west of the alleged vicariant division and antedating its occurrence. Perhaps middle Miocene orogenic activity involving the same landscape was responsible, though both these scenarios are highly speculative.

THE QUATERNARY PERIOD

The Pleistocene Epoch

Local extinction, fragmentation, and limited dispersal characterize the Quaternary history of the gopher tortoises, unlike the vigorous speciation and expansion of the Tertiary. However, few of the Pleistocene fossils are assigned absolute dates. Available data inscribe only possible distribution, and many have recently been taxonomically reassessed (King and Saunders, 1986). The situation is further confused by uncertain taxonomic relationships of several closely related fossil *Gopherus*. The Pleistocene section summarizes the geographical distribution of *G. flavomarginatus*, describes the paleoecological setting for this distribution, accounts for the Pleistocene and Holocene ecological changes that led to the fragmented modern distribution, and addresses the issue of late Pleistocene mass extinction of the North American megafauna.

Middle to late Pleistocene *G. auffenbergi* (= *berlandieri*) have been reported from Aguascalientes, Mexico (Mooser, 1972), and fossils resembling *G. canyonensis* and/or *G. flavomarginatus* from Phoenix and El Mirage (Bramble, 1982; T. Van Devender, personal communication). D. Bramble (personal communication) observed that the Phoenix fossils appear to be late Pleistocene (Rancholabrean?), based upon their stratigraphic position. Auffenberg (1969) described the Pleistocene range of *G. flavomarginatus* as almost all of the Mexican Plateau, extending at least from southern New Mexico south to Aguascalientes. He further noted a specimen from the middle Pleistocene of Kansas that was structurally similar to both *G. flavomarginatus* and *G. polyphemus*. Maximal distribution was probably achieved in the late Pliocene and was reduced progressively in the first half of the Pleistocene by orogeny in the south. Little is known about the paleoecology of the sites from which these fossils have been reported.

In light of the Pleistocene range of *C. flavomarginatus*, the paleoecology of the Mexican Plateau and adjacent basin and range topography, especially the northern and western parts, will be emphasized. It is also important to note two recent revisions in Quaternary perspectives that greatly influence this account. First, Imbrie and Imbrie (1980), based largely on oxygen 16/18 ratios, proposed that the Pleistocene was subject to 15–20 glacial pulses. Each episode lasted about 90,000 years and had about 10,000 years of interglacial stage. This discovery not only increases the number of Pleistocene alternating climatic intervals in North America to 15–20, but also reduces interglacial episodes to a maximum of 10% of the last two million years, and more likely to 6% (Van Devender, 1986).

The second revision of Pleistocene perspective results largely from analysis of late Pleistocene packrat (*Neotoma*) middens (Van Devender, 1976, 1977, 1978,

1986; Van Devender and Mead, 1978; Van Devender and Spaulding, 1979). Data from middens extending across several North American deserts document that downslope displacement of piñon-juniper woodland due to increasingly cool climate was not universal, nor did a reciprocal replacement of more xeric-adapted species always occur. These discoveries challenge simplistic models that invoke unified and exclusionary displacements of tightly coevolved Pleistocene communities. The glaciopluvial communities described by Van Devender often bore more resemblance in organization to contemporary tropical communities, manifest by high diversity, the presence of more southern taxa, and intercommunity transitions characterized by gradual climatic gradients formed by species specific changes, not by narrow discrete ecotonal boundaries. Thus, these glaciopluvial assemblages may well represent the "norm" for the Quaternary. However, Brackenridge (1978) and Spaulding and Graumlich (1986) questioned this scenario for equability, particularly for the more western (Nevada) desert regions. Modern associations are best treated as temporary and probably short-lived interglacial anomalies. An ecological characterization of the glaciopluvial Mexican Plateau (north of the Transvolcanic Province) is completed by examination of the major, current biotic subprovinces of the Chihuahuan Desert (Morafka 1978): the northern Trans-Pecos (Rio Grande drainage), the central Mapimian, and the southern Saladan.

Pollen analyses from New Mexico (Hafsten, 1961) reveal the fossil record in mild interglacial Wisconsin times. These analyses, when combined with midden records, span the longitudinal axis of the Trans-Pecos Subprovince of the northern Chihuahuan Desert. Cool, moist grasslands, either treeless or with poorly developed pine "parkland" dominated lower elevations (Llano Estacado) of interglacial (33,500 to 22,000 years ago) with vegetation of spruce (*Picea*) and pine (*Pinus*) woodlands at least in upland situations, accompanied by juniper-oak-piñon woodlands and grasslands in lower basins. End-Pleistocene habitats (15,000 to 10,000 years ago) continued to sustain piñon woodlands and oak/grass. Cold scrub (*Artemisia*) probably locally dominated dry slopes and dunes (Harris, 1978) and remained serially dominant even into early Holocene times at least in the northwestern Trans-Pecos extending south specifically to the Hueco Mountains (Texas) according to Van Devender et al. (1987). Evidence from midden and fossil data generally corroborate the reconstruction of glacial Trans-Pecos habitats as cooler in the summer, with more abundant precipitation evenly distributed throughout the year, and less extreme summer and winter temperatures than found today.

The Pleistocene history of the Mapimian Subprovince is based primarily on a pair of midden localities at the eastern edge of the Mapimi bolsons, and a pollen history from Cuatro Ciénegas at the eastern edge of the region. Van Devender and Burgess (1985) discovered a wood rat midden from the Sierra de la Misericordia (near Bermejillo), Durango, showing a past flora of essentially modern desert perennials, of which 50% were succulents. Seventy to 100% of these species currently occur within 1 km of the midden site. However, the reverse was true of trees and woody shrubs. A well-developed piñon-juniper woodland was recorded at this site. Species currently extralimital to this area were derived from all directions, but the largest components came from the south and east. A similar east-to-west expansion of Pleistocene biota has been described for the herpetofauna by Auffenberg and Milstead (1965) and Morafka (1978).

Palynological studies of the past 20,000 years in the Cuatro Ciénegas Basin, Coahuila (Meyer, 1973), concluded that the vegetation (Desert Woodland) re-

mained essentially unchanged at lower elevations. Limited midden data from the same region (Van Devender and Burgess, 1985) also yielded some desert flora during late Pleistocene times, but mixed with a significant piñon-juniper component.

Relative to the Trans-Pecos floras, the cooler, mesic woodland assemblages of the Mapimian were probably influenced by even greater equability in temperature (more sheltered from "blue northers") and by more evenly distributed precipitation, especially in winter (Van Devender and Burgess, 1985). In contrast, survival of heliothermic endemic desert lizards such as *Uma exsul* (Pough et al., 1978) along with succulents indicates that sandy and rocky substrates in hot, exposed and well-drained edaphic patches probably persisted throughout the Pleistocene. These taxa survived in warm microclimates through major cooling climatic trends which resulted in lower elevation limits of piñon woodland. Because of the downward superimposition of these woodlands, Van Devender and Burgess (1985) rejected the Mapimi bolson as a refugium for desert biota, based on the mixed nature of the glacial flora relative to modern "pure" desert associations. Refugia, however, do not require survival of a completely intact relict ecosystem. When the Mapimi flora is compared to its widespread Tertiary precursor (at least at the generic level), the Mojavia flora of Axelrod (1958), the Mapimi bolson emerges as a significant, if differential, refugium (Morafka and Lieberman, in press).

Almost nothing is known about Pleistocene conditions in the southern Saladan Subprovince of the Chihuahuan Desert. Harris (1978) described southward range extension of the marmot (*Marmota* sp.), based on Pleistocene fossils from San Josecito Cave in Nuevo Leon (on the periphery of the Saladan Subprovince). He interpreted its presence as indicating increased moisture during winter and spring. Van Devender (personal communication) reported a more extensive small mammal fauna from the same site, including Rocky Mountain, midwestern and tropical species. The high, 1500 to 2000 m minimum relief of the Saladan plains did not favor maintenance of a refugial desert. A few generalized desert species may have survived in complex mild-cool adapted communities of piñon-juniper-oak woodland, chaparral and occasional grassland, paralleling isochronous conditions in the high, cold Great Basin (Mead et al., 1982).

Pliocene climates and topography fostered ecological conditions conducive to a more continuous and extensive distribution for *G. flavomarginatus*, possibly including most of the Mexican Plateau north of the Transvolcanic Axis and north into Texas, New Mexico, and southeastern Arizona. That range has been progressively fragmented and reduced. By the early Pleistocene it may have been reduced to the sites of Trans-Pecos and Mapimi—subprovinces of the modern Chihuahuan Desert. Regional geology presents two interrelated agents with potential for both topographical and ecological fragmentation and extirpation: faulting and lake development. The former was already episodically important throughout Mio-Pliocene periods possibly peaking in the Plio-early Pleistocene.

While the Sierras and Mexican Plateau were largely Oligocene (Oriental) and Miocene (Occidental) in their orogenies (McDowell and Keizer, 1977), there were widespread episodes of mountain rejuvenation throughout the southwest during the late Pliocene and early Pleistocene (King, 1959; Cooper and Silver, 1976; Strain, 1966; Maxwell et al., 1967; Arellano, 1951). Widespread secondary faulting of existing mountain blocks accentuated the basin and range topography that dominates this region. Belcher (1975), among others, has summarized the tectonic

events which led to the evolution of the Rio Grande Rift. Repeated faulting of this landscape does not appear to have excluded *Gopherus* despite the suggestion of Bramble (personal communication) that this would be the case. These processes resulted in closed drainage systems (bolsons) which filled during glaciopluvial precipitation. Rainfall probably increased under these climatic regimes, and standing water had less evaporative loss. Van Devender (1986) suggested that winter precipitation was significant. Furthermore, not all water in these bolsons was from local precipitation. Watersheds in the Rocky Mountains and Sierra Madre Occidental drained to the east of the Continental Divide and produced some of the largest regional lakes. Until the middle Pleistocene, the Rio Grande (the now dominant river of the Trans-Pecos) was a closed basin drainage, terminating in the large playas (lagunas Santa Maria, Palomas, and Guzman) of northwest Chihuahua (Hawley, 1969; Reeves, 1969). Other major glaciopluvial lakes of that northern subprovince included the Estancia Basin, Tularosa Basin, Plains of San Augustin, the Animas and Playas valleys of New Mexico (Kottlewski, 1958), and the Willcox Playa in southeastern Arizona. The Mapimian core of the Plateau also had major lakes in most of its bolsons (Van Devender, 1978). Of particular interest, a massive lake connected the now dry playas of Laguna de Palomas, southeast Chihuahua and Durango (not to be confused with the playa of the same name in northwest Chihuahua) with Coahuila's Laguna del Rey (J. Bartolino, personal communication). As noted previously this combined body of water probably separated the Remedios and Diablo populations of *G. flavomarginatus* intermittently from those south of the lake in what is now the Mapimi core district. Limestone ranges (interspersed with extensive Miocene igneous deposits in the west) combined with bolson lakes to sequester small, isolated tortoise populations along Pleistocene lake shorelines, as illustrated in Fig. 19. Furthermore, the valleys immediately south and east of the Mapimi tortoise district appear to have had extensive flooding, presumably from Laguna Mayran that extended northward toward Tlahualilo and filled (or spilled over into) the Valle de Acatita, Durango. This latter valley is just south and east of the limestone ridges that terminate the Mapimi District. Freshwater mussel shells are found in the extensive sand dunes of the Valle de Acatita, while these sands lack fringe toed lizards (*Uma*) that dominate hummocks both north and south of the Valle. Mussel fragments occur also in the open dunes of Laguna Mayran still occupied by *Uma exsul*. However, Valle de Acatita, unlike Laguna Mayran, is a very narrow and steep walled trough. This region still harbors mud flats and reeds at Los Charcos de Risa. Presumably, the valley was completely inundated by a Pleistocene lake.

Northeast of the Americanos District, the Llano del Guaje appears to be another former wetland barrier. This huge plain borders tortoise populations northeast of Laguna de la Leche, below the north slope of Sierra San Francisco. Almost uniform *Hilaria mutica* grassland covers much of northwestern Coahuila, stretching east to the uplands surrounding Ocampo, and north virtually to the Sierra del Carmen—Big Bend region of the Rio Grande. These plains were probably a marshland or flooded grassland during glaciopluvial times. They may have received heavy summer monsoon rains originating in the Gulf of Mexico (Wells, 1979), if this controversial hypothesis is correct. Even if rainfall cycles and patterns were different, any net increase in precipitation might have produced the immense swale grassland suggested. Today, flooded conditions are somewhat replicated during the summer wet season. Silty soils in the Llano del Guaje also indicate a history of standing flood waters. Farther south, both the Sierra Madre ranges plus the

GLACIOPLUVIAL DESERT REFUGIA

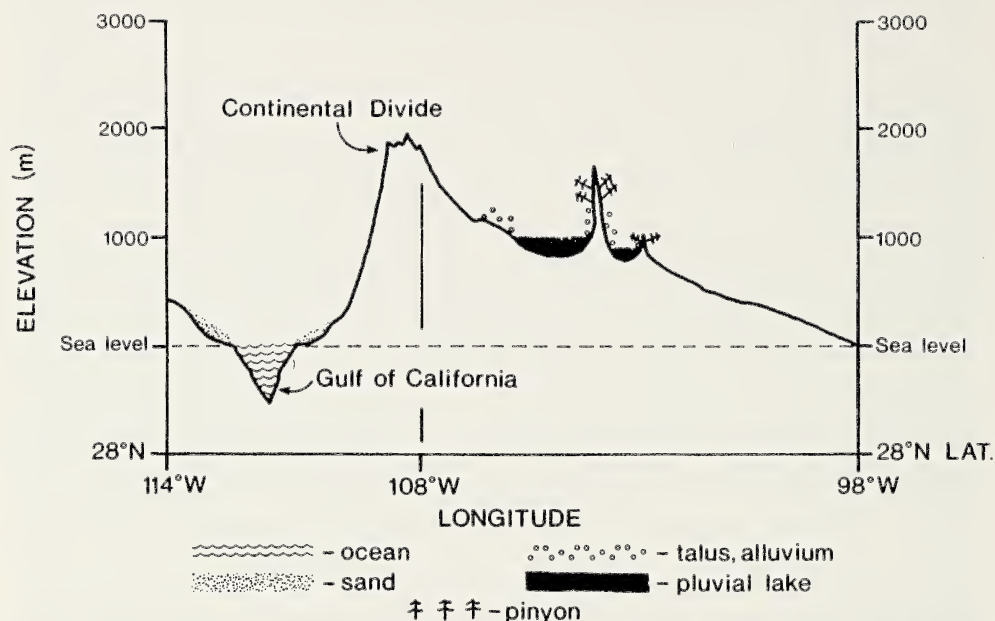


Fig. 19.—Cross-sectional diagram of glaciopluvial North America at the 26th Parallel North, which provides a diagrammatic depiction of the regional fragmentation of the Mapimi refugium.

transverse Anticlinorium of Arteaga fed the lake system of the Parras Basin, which includes the present day lagunas Mayran and Viesca. Despite this double barrier of lakes and 500–1000 m limestone ridges, *G. flavomarginatus* ranged to Aguascalientes, far to the south, possibly during the mid to late Pleistocene (Auffenberg and Franz, 1978). Such a distribution might have been established during Pliocene periods of lower elevation in the Saladan portion of the Plateau (Arellano, 1951), or by a later access to the south along the low Nazas-Aguanaval river valleys bordering the western side of the Parras Basin, where the adjoining uplift (Anticlinorium of Arteaga) is reduced in both elevation and continuity (Cohn, 1965; Morafka, 1978).

The Holocene Epoch

This Holocene Epoch is essentially the last interglacial, representing only a 11,000 year instant within the 1.8 million year old Quaternary. Nonetheless, the Holocene climatic sequence probably recapitulates all of the paleoecological transformations of the 15 to 20 interglacials that punctuated the Pleistocene. In fact, Van Devender (1986) suggested that the Holocene sequence of vegetational replacements in the Chihuahuan Desert may have recapitulated the late Tertiary pattern by which this ecosystem originally developed.

As in the Pleistocene account, any characterization of the region during the Holocene must consider differences between the three Chihuahuan subprovinces. Van Devender (1986) describes the sequence for the Trans-Pecos Subprovince as "... the early Holocene 11,000 to 8,000 years vegetation was a transitional xeric

oak-juniper woodland (Van Devender, 1977). The middle Holocene was a desert-grassland period lacking both woodland and many important Chihuahuan Desert scrub plants. Development of the modern communities was in all cases a late Holocene event. The vegetation changes that mark the boundaries between the early, middle and late Holocene have some temporal variability but were completed 8,000 and 4,000 years ago, respectively."

Van Devender modified this chronology for a Mapimian Subprovince site at Rio Grande Village (Big Bend National Park, Texas) in noting that xeric-adapted Chihuahuan species were already important in Late Wisconsin time, and that the development of desert-grassland was an Early, rather than Middle Holocene event. Messing (1986) noted Pleistocene-Holocene *G. flavomarginatus* from a now extralimital Mapimian site near Jimenez, Chihuahua.

There is no fossil evidence from the Pre-Columbian Holocene of the southern, Saladan Subprovince. Again, by extrapolation from higher elevations and the recently derived desert herpetofauna, its Holocene history, like that of the Trans-Pecos, was presumably marked by reinvasion of desert biota from the Mapimian Subprovince.

Van Devender (1986) indicated that modernization of Holocene plant communities was a stepwise process. Earlier, Van Devender (1978) referred to glaciopluvial conditions, indicating a strong continuity between late Wisconsin and early Holocene conditions (for example, the continuation of widespread piñon-juniper woodlands at lower elevations). Van Devender's middle Holocene "monsoonal" and the Altithermal period (of Antevs, 1948) would appear to be diametrically opposed in their climatic connotations. Van Devender and Worthington (1978) reported no evidence of a hot, dry Altithermal during the middle Holocene at a site near Deming, New Mexico, at the northwest edge of the Chihuahuan Desert. Similarly, Bryant (1978) reported only erosional (no palynological) evidence for an Altithermal climate from the northeastern edge of the Chihuahuan Desert near Del Rio, Texas. Instead, a monsoonal episode may have occurred characterized by strong summer rains from the Gulf of Mexico and gradually warming climates conducive to grassland development. In fact, the conflict is more apparent than real. In all cases, Altithermal correlates with higher middle Holocene temperatures. These induce aridity in the absence of monsoonal precipitation but stimulated them in more mesic/eastern areas where summer rains were already established. Apparently, these same warming trends continued in the Great Basin and Great Plains, areas peripheral to the Mexican Plateau, without the intervention of monsoonal precipitation. In these latter regions, Altithermal warmth and aridity exceeded modern conditions. Van Devender and Worthington (1978) reported that a warm, xeric episode occurred in the late Holocene of southern New Mexico. The delay or suppression of Holocene aridity in the Chihuahuan Desert region by these monsoonal storm tracks is an important consideration in evaluating alternative hypotheses explaining mass extinction of large vertebrates that coincided with the early Holocene. The varying seasonality of altithermals further complicates the correlation of peak arid episodes between regions generally (Davis, 1984). This poses special difficulties for those wishing to invoke climatic change as the common denominator of the extensive and relatively isochronous extinction of the southwestern megafauna. The most dramatic deterioration of regional glaciopluvial equability and grassland vegetation probably occurred only 4000 years ago, long after the demise of the megafauna. However, these latter changes may play an important role in accounting for local extirpation of *G. flavomarginatus*.

QUATERNARY EXTINCTIONS

During the latest millennium (Wisconsin Glacial), there was a relatively sudden mass extinction of the North American megafauna, removing the majority of larger (44–50 kg) herbivores and their dependent predators from the continent's ecosystems. Even viewed in the larger context of Cenozoic extinction episodes (Webb, 1984) and species turnover rates (Gingerich, 1984), the scope, size-based specificity, and temporal brevity (intensity) of this one extinction episode appear to be unique. Reviews of both hypothetical causes and empirically assessed results of these extinctions are provided by Martin (1967) and the contributions to Martin and Klein (1984). Marshall (1984) provided a particularly lucid overview of the issues, evidence, and the special nomenclature devised to represent them.

The Quaternary megafaunal extinction episode is especially relevant to *G. flavomarginatus* distribution since the morphology, ecology, and vulnerable behavior of the species (criteria from Martin, 1984a) clearly establish it as a member of the collapsing megafauna. Based upon the fossil conspecific *Gopherus* "*huecoensis*" and the *polyphemus*-like ally *G. canyonensis*, isometric predecessors of *G. flavomarginatus* might have been twice the size (linear measurement) and eight times the mass (possibly up to 160 kg) of extant *Gopherus*. As grassland herbivores, tortoises are also similar ecologically to many of the now extinct mammalian megafauna. This tortoise appears to have suffered a recent, rapid, and massive extirpation, from perhaps 80% of its Pleistocene range, even after end Tertiary orogenic reductions to the south are taken into account. Its extirpation may have been paralleled by Holocene diminution of size, very much the parallel of its mammalian analogs.

A wide array of both complementary and contradictory theories have emerged regarding the megafaunal extinctions in North America, and globally. These are: (i) Disease and other pathology based models; (ii) Climatic/ecogeographical models; and (iii) Predation (non-human or human, including the "Pleistocene overkill" hypothesis). Here, we attempt to define each model as it applies specifically to *G. flavomarginatus*. The Bolson tortoise, as a megafaunal component now in the twilight of its survival, provides an interesting test case of the appropriateness of these hypotheses.

Disease

Disease and pathological causes are of more historical interest than practical value. At least for North America, there have been few recorded invasions by potential disease vectors in the later Pleistocene other than *Homo sapiens* and the musk ox (*Ovibos*), mammoth (*Mammuthus*), and the bison (*Bison*) which may have made a mid-Pleistocene entrance to North America (Martin, 1967). Paleolithic hunters who entered North America were not a major reservoir of Old World diseases (Hare, 1967). It is unlikely that a single pathogen or even suite of agents would differentially infect large animals regardless of taxon (mammal, bird, and reptile), and spare smaller, more closely-related host species.

Veterinary diagnostic panels for *G. flavomarginatus* blood chemistry and cell differentials, and fecal flotations for parasite (nematode) eggs have revealed no significant pathologies among 50 wild tortoises monitored at the Mapimi laboratory (Morafka et al., 1986). Monitored values were generally within the known ranges of healthy *G. agassizii* (Lieberman and Rosskopf, 1986), even in *G. flavomarginatus* bearing fairly heavy nematode loads (Adest et al., in press).

Similar arguments may be employed in eliminating reproductive or developmental defects (Neuville, 1921; McClean, 1981). Given the diversity of the megafauna, the absence of evidence either past or present, and the uncertainty of climatic extremes that allegedly induced pathologies, defects do not seem a likely explanation. There were few extinctions during the previous 15–20 glacial episodes, thus climate-induced physiological catastrophes appear improbable. In any case such reproductive health models are only credible for mammals with long gestation periods and low fecundity (Kiltie, 1984); neither condition applies to tortoises.

Climate

McClean (1981) linked gestation failure and general physiological failure to hotter summers than either glacial or contemporary climates could produce. The effect of “hot” (and dry) summers was also hypothesized for megafauna extinctions in central Texas (Lundelius, 1967). This simple climatic model invoked reduced equability: higher and drier annual averages than at present, and greater seasonality. Such scenarios depend upon setting major megafauna extinctions at about 8000 years ago, synchronous with the beginning middle Holocene. Geochronology provides little or no support for this hypothesis. When the middle Holocene Altithermal took place, 3000 years after the peak of extinctions, it was regionally specific in its effect. As already observed, Van Devender and Worthington (1978) and Bryant (1978) indicated no vegetational evidence for a New Mexico–West Texas Altithermal. Rather, they found an expansion of the grasslands for which many of the extinct megafaunal species were well-adapted (Mehring, 1967; McDonald, 1984).

An alternative cold summer shock hypothesis was developed by Axelrod (1967). Its central theme was increased mortality of mammalian herbivore calves in the Great Plains due to polar summer storms moving south through the midcontinental aperture developing between the deteriorating Laurentide and Cordilleran glaciers. A wide variety of large herbivores would have been affected, just as are cattle in the northern plains today. However, the hypothesis does not clarify why climatically sheltered coastal populations (for example, the Rancho la Brea fauna in California), as well as those in the Mexican Plateau and American tropics were simultaneously affected (McDonald, 1984), nor does it explain why equally extreme interglacials (120,000 and 320,000 years ago; Covey, 1984) failed to produce similar results.

The third model for a Holocene climatic catastrophe is the “blue norther.” As in the previous hypothesis, the mid-continental recession of the Laurentide and Cordilleran glaciers opened a southward path for severe polar storms, but in this case the emphasis is placed on winter, rather than summer episodes (Bryson and Wendland, 1967). Unlike the previous explanations, considerable geological and climatological evidence documents inland deterioration of the continental glacier and, consequently, increased seasonality. Harsher winters probably characterized the early and middle Holocene in the middle latitudes and longitudes of North America (Bryson et al., 1969). Furthermore, Van Devender et al. (1976) and Moodie and Van Devender (1979) linked this climatic change directly to the early Holocene extirpation of several chelonians from what is now the New Mexico–western Trans-Pecos region. They suggested climatic extirpation of *Gopherus agassizii*, *Geochelone wilsoni*, and *Terrapene carolina putnami* from the northern Chihuahuan Desert. Prior to the Holocene extirpations, they projected continuous

distributions for *G. agassizii*, *G. berlandieri* and *G. flavomarginatus*. They tentatively attribute primary extirpation of tortoises to colder winters, but do not exclude related vegetational changes or the simultaneous southward advance of Paleo-Indian predators. Of all the Holocene climatic factors proposed, minimum winter temperatures correspond most strongly with current northern limits of tortoises (especially *G. agassizii*). *Gopherus flavomarginatus* were probably tolerant of some cold winters given both their 10-year survival and natural reproduction in a captive population at the Research Ranch, Elgin, Arizona (Appleton, 1978). This site is located in oak grassland habitat at 1500 m elevation. Lowe et al. (1971) documented considerable supercooling capacities for *G. berlandieri* (-5.25°C). However, if severe polar storms ("blue northers") did bring hard frosts and snow precipitation, lethal freezing might penetrate even into some burrows, particularly killing hatchlings in their more shallow shelters.

Although these storms may penetrate farther south, even to Mexico City, their duration is more limited. The incursion of northers beyond the Trans-Pecos into the Mapimian refugium was probably a much less frequent event and the effect on local climatic conditions less severe than suggested, as they would have been dissipated by intervening transverse ranges (Davis Mountains), lower latitudes, and lower elevations. Hadley's Cell, a stable subtropical high pressure air mass, may have deflected storms far to the south (Gates, 1976), though early models projecting the climatology of the last glacial, may have underestimated cooling at lower latitudes, a factor which could have eliminated the cell.

Vegetational Changes

Accompanying these climatic scenarios of mass extinction are several secondary effects, especially vegetation changes. These ecogeographical explanations synthesize climatic, vegetational, and faunal evolutionary evidence in various ways, but there is one unifying theme: glaciopluvial communities were restructured and individual species displaced drastically and in unique ways at the end of the Pleistocene. As a result, coevolved stability was thrown into disequilibrium in the new depauperate Holocene communities (Graham and Lundelius, 1984). Ensuing disruptions of food webs resulted in faunal collapses involving both large and small species. Empirical evidence for the previous existence of stable coevolved communities is scant. Already noted, Spaulding and Martin (1979) provide evidence for the opposite. Van Devender et al. (1976) argued effectively against the assumption of static community concepts in their analysis of a Trans-Pecos fossil flora. In a genetically explicit analysis of Baja California herpetofaunal biogeography, Murphy (1983) rejected general application of coevolution in explaining past or present biotic assemblages. For example, the entire southwestern desert biota evolved without its current dominant shrub, creosote (*Larrea divaricata*), which is probably a late invader of North America arriving from Patagonia during some undetermined interglacial or even in the Wisconsin Glacial.

An alternative version of the ecological synthesis has been presented by Guthrie (1984, based in part upon Leopold, 1967), who developed a suite of possible coevolved herbivore to vegetation form dependencies. He suggests that the Holocene was a unique "interglacial," where originally complex Pleistocene floral mosaics were reduced to species-poor zones. The consequence was nutritional inadequacy of locally available forage, combined with reduced primary growing seasons resulting from less equability in climate. Again, little fossil or contemporary supportive evidence exists, especially from regions (for example, Mexico)

of southern North America. Modern Mapimian plant associations sustain a complex mosaic of species, reflecting the continuing equability of the region. Studies of the natural diet of *G. flavomarginatus* (Adest et al., in press) indicate adequate high-protein forage from Mapimi localities which are not overgrazed. The tortoise survives well on a variety of grasses and forbs, provided that protein content (16%) in the juvenile diet is adequate.

G. flavomarginatus is a grazer/browser that underwent a Wisconsin-Holocene collapse in distribution, presumably concomitantly with the rest of the megafauna. However, our previous review offers no evidence for alteration of end Pleistocene habitats sufficient to threaten food availability for *G. flavomarginatus*. McDonald (1984) estimated that North American grassland productivity may have undergone a 75% increase during the very time of most megafaunal extinctions. Despite the logical and theoretical attractiveness of synthetic models for extinction, they are probably more appropriate for accounts of progressive individual species extirpation than for the sudden demise of such diverse megafauna. On the other hand, the late Holocene (last 4000 yr) reduction of Trans-Pecos grasslands might have locally extirpated *G. flavomarginatus*. The impact may have been even greater if we assume that vegetational shifts to coarse sand/gravel scrubland favored competitive exclusion of *G. flavomarginatus* by the more xeric-adapted "*Xerobates*" (*G. agassizii/berlandieri*) of Bramble (1982). Ultimately, both climatic and vegetational models of Holocene extinction are extremely vulnerable to the argument that these events were no more severe (hot/cold) than at least three of the preceding 15–20 interglacials (McDonald, 1984) which produced no comparable extinctions.

Predation

Non-human predation has no empirical basis as a factor in North American Pleistocene extinctions. No single carnivore has emerged as a candidate, and none suddenly appeared or expanded near the time of extinctions. Peak aridity and recent overgrazing may have reduced ground cover so severely as to expose hatchlings to greater predation, but objective demonstration of this has yet to take place.

By elimination of other factors, human induced extinction remains among the few plausible explanations. Further, it has the most explicit fossil evidence as well as a convincing causal relationship still operative in contemporary times.

The timing and geography of Pleistocene extinctions that associate tortoises and human invasion are coupled with a "*modus operandi*" that is distinctly human in character. Circumstantial evidence implies that Paleolithic hunters (Paleo-Indian) are the primary cause of megafauna extinctions. Human hunters may have accentuated extirpations and fragmentations typical of the interglacials into catastrophes from which no subsequent recovery was possible. Six major arguments support the decisive role of human predators in this most abrupt North American extinction:

(1) *Chronology*.—Martin (1958, 1967, 1984b) emphasized a sudden mass extinction of the North American megafauna at 11,000 years ago. This peak, spanning perhaps a thousand years, has been tentatively corroborated by Marcus and Berger (1984) and Mead and Meltzer (1984).

Almost no unambiguous record for humans in North America extends beyond 13,000 years. While MacNeish (1976) and Dillehay (1984) had attempted to establish earlier dates, Berger (1980), and Adovasio and Carlisle (1984) identified

only a single Pennsylvania site (about 19,000 years old) significantly older than the Pleistocene-Holocene boundary. Even the antiquity of this site has been challenged (Mead, 1980). Most evidence indicates several waves of Paleo-Indian invaders from Asia between 14,000 and 8000 years ago and most, if not all, moved south through the mid-Continental corridor (Great Plains) between the Laurentide and Cordilleran glacial masses. After initial human dispersal, some latency period must have taken place before human distribution, density, technology and strategies were sufficient to have major effects. If this assumption is correct, first occurrence of New World humans is not as critical to overkill hypotheses as are their densities and cultural stages. MacNeish (1976), who did not subscribe to the human overkill scenario, still recognized multistage increments in human impact. When differences in reported dates and interpretations are reconciled, the first widespread establishment of human populations in North America correlates well with the demise of the native megafauna. Furthermore, human population establishment is the unique factor which distinguishes the end of the Wisconsin Glacial from several equally severe precursors.

(2) *Geography*.—Geography provides evidence in support of Martin's overkill hypothesis and contradicts climatic alternatives. Geographically, megafaunal extinction occurred only where humans made a sudden first appearance in the Holocene (or very end of the Wisconsin Glacial). In the New World, extinction of the megafauna moved in a north (Bering Strait) to south (Patagonia) wave between 12,000 and 8000 years ago (Martin, 1967), as would be expected if human predation were causal. No climatic or ecological alternative has been suggested that would produce the same pattern.

Insular extinctions in the late Holocene are exceptions that support the overkill rule. Flightless New Zealand and Malagasy birds (Battistini and Verin, 1967; Cassels, 1984) and the larger Malagasy lemuroids and tortoises (Walker, 1967; Dewar, 1984) were refugial insular megafauna subjected to later human invasions. Large tortoises (*Geochelone*) were also subject to these later invasions and extinctions on islands such as Cuba and Mona Island (Williams, 1950, 1952), the Celebes and Malta (Martin, 1967, 1984a) and in historical times, the Galapagos. Giant tortoise populations on Aldabra Island in the Indian Ocean might be viewed as a historical control to the Galapagos experience. In less than 200 years, the Galapagos *Geochelone* suffered a massive decline as a result of human predation and the introduction of rats, dogs, and goats. In contrast, the Aldabra tortoise population remains vigorous on an island that has been spared human intrusion during the 20th century by virtue of the island's lack of harbors, presence of impenetrable scrub, and remote position (Swingland, personal communication; Pritchard, 1979). Again, no climatic-vegetational model rivals the human factor as a common denominator of this global array of Holocene insular extinctions. Only one recently extinct horned "tortoise" (*Meiolania*), from Lord Howe Island in the Australian Realm, appears to have been extinguished by climatic causes, possibly inundation (Martin, 1984a).

(3) *Susceptibility*.—Large slow grazers and browsers appear to have been relatively easy prey for Paleolithic hunters. In North America, mammoths were initially the target species, later replaced by archaic bison (consisting of larger antecedents of existing *Bison* according to some authorities, but including two extinct species in the view of others), and ultimately by the surviving *Bison bison* (Reeves, 1983; Frison and Stanford, 1982; Davis and Wilson, 1978). Selection for large size characterized Paleo-Indian hunting preferences between species and within

species (Edwards, 1967). Chelonians and their eggs were part of the exploited megafauna in the American Southwest. Moodie and Van Devender (1979) reported tortoise shells in association with the artifacts of Paleo-Indians. Fossil tortoises (*Geochelone*) from Florida sinkholes have bone fractures caused by humans, and have been found in association with Paleo-Indian artifacts (Canby, 1979; Holman and Clausen, 1984). Similarly, temperate North America's largest land reptile (*G. flavomarginatus*) is also the most endangered tortoise due to direct human predation. Shell lengths in some *Gopherus* lineages have become reduced by one-half to two-thirds since late Pleistocene times. Edwards (1967) reported that size reduction in response to cooler climates might be expected in heliothermic reptiles, and the opposite should be true for most homeothermic megafauna. However, Van Devender (personal communication) concluded the equable climates of the glacials (mild winters) did favor larger size. The Holocene record has witnessed simultaneous diminution in lineages (*Bufo*, *Sceloporus*, *Procyon*—Van Devender, personal communication) of many physiological types, through varied climates, possibly due to human selection in some taxa, but certainly not in all (*Bufo*). Marshall (1984) proposed a strong correlation between diminution and extinction. King and Saunders (1984) interpreted such a correlation in mastodon chronoclines as the result of "island effects in relictual distribution patterns." However, Shine (1986) and Kowarsky (1982) documented aboriginal human predation directed differentially against larger (female) snakes (*Acrochordus*) and sea turtles, respectively.

Behavioral vulnerability has also been suggested as affecting the extinct megafauna. Clear documentation of such vulnerability in North American bison (assigned to two extinct, one extinct and/or one living species by different authorities) has been provided by Reeves (1983). Search images, sound cues, and scents which alerted large prey to native predators may not have provided adequate cues to escape human hunters. Certainly tortoises caught away from burrows would have been extremely vulnerable. Based on our estimations of shell strength, and extrapolations from other species, adult shells are adequate defense against most present carnivores (coyotes, foxes, raptors) except the very largest, such as the puma (Moskowitz, personal communication). But these were useless against even the most elemental hunting implements. In fact, tortoises may have even attracted attacks because of the utility of their shells as containers (even today they are used as water bowls and chicken feeders). Taylor (1982) documented parallel modern human exploitation of *G. polyphemus* in north central Florida. However, the burrow provided significant defense. Its extreme depth of two meters or more (Morafka, 1982) is adequate protection against surface predators, even formidable carnivores (for example, bears) that are no longer extant within the range of tortoises. Possibly these long burrows account for the survival of *Gopherus flavomarginatus* while the more widespread but surface-dwelling tortoises (*Geochelone*) became extinct in North America. In apparent contradiction to this line of logic, it might be argued that both *G. agassizii* and *G. berlandieri* are smaller, weaker, more surface active, less protected by deep burrows, and therefore more attractive as potential prey for humans. Why then have they not suffered extinction before the more formidable *G. flavomarginatus*? Human predation typically selects biggest game first, both within and among species. Furthermore, bigger animals often have smaller populations with lower replacement rates. Finally, *G. flavomarginatus* may simply have tasted better and/or yielded more meat than the other members of its genus. Even the differential effects of tribal taboos may

have favored one species over another. Such eclectic selectivity has been exhibited by aboriginal hunters in South America. Some tribes select *Geochelone carbonaria* while others prey only upon the syntopic *G. denticulata* (Moskowitz, personal communication, 1986).

(4) *Lack of ecological replacement.*—In most ecological communities, a declining species is displaced by a more successful competitor or subsequently replaced by an ecological equivalent. This has not occurred in the North American megafauna. Introduction of domestic livestock obscures the truly depauperate condition of native North American megafauna. New or different species should be expected to disperse from adjacent habitats or increase in density in order to exploit the newly available habitat. A terrestrial box turtle (*Terrapene ornata luteola*) now occupies much of the former range of *G. flavomarginatus* in the Trans-Pecos Subprovince of the Chihuahuan Desert. However, this small-sized omnivore in no way fills the burrowing-grazer niche left unoccupied by the extirpated tortoises.

(5) *Human population dynamics.*—Previous quantitative models have shown marked human population growth, oscillations, dispersal, and predation pressure in Paleolithic North America (Martin, 1973; Mosimann and Martin, 1975; Whittington and Dyke, 1984). Although the specific initiation times and patterns of these events have been questioned (Davis, 1978), the models demonstrate the human populations had the potential to grow, disperse, and prey upon the megafauna at rates adequate to explain a mass extinction across the New World in only 2000 years. The validity of the overkill hypothesis does not rest upon these models, but they do enhance its credibility as physically feasible. The credibility of the “overkill/blitzkrieg” hypothesis has been further advanced in this instance by the estimates of Carroll (1968) that 300,000 families occupied the “Great Bolson” of the Chihuahuan Desert (upper Rio Grande Valley) in Pre-Columbian times. Ware (1984) also suggests a 10,000 year human presence in the Rio Grande Valley, characterized by maize-based agriculture for the last 2000 years, presumably conducive to larger resident populations.

Humans are adaptable omnivores and, in the presence of a negative feedback system (especially agricultural societies) that may keep some specialized carnivores in equilibrium with prey, human predation pressure may go unchecked. Because alternative food sources are generally diverse and may be stored, human pressure might have been unrelenting, ultimately causing the extinction of prey populations.

(6) *The uniformitarian argument: human hunter-gatherers in historic times.*—Modern history has recorded frequent and consistent extirpations and extinctions as a result of human predation on large animals. Grizzly bears, condors, and bison appear to have been the last in a series of target species for human hunters in the Southwest. Diamond (1984) provided an excellent set of case studies and patterns of human-induced extinctions that have occurred in historic times. Perhaps the best modern analogue to human invasion of the New World, is our current exploitation of the oceans. At sea, humans still operate as vagrant hunter-gatherers, using essentially refined (and only recently mechanized) snares, nets and spears. The impact of small and temporary human populations has brought about annihilation of the marine megafauna (ranging from auks to sea cows, and the various cetaceans). Just as on land, large sea turtles have not been exempt; their eggs are removed from shore nests while adults are harpooned at sea.

POST-COLUMBIAN EVENTS

The historical record for the Mapimian region in north central Mexico is confined to the past 450 years. The major events of this history include the intro-

duction of European people, plants and livestock, and elimination of native hunter-gatherers since 1900. There has been the increasing collection of native plants, in particular, the wax plant, candelilla (*Euphorbia antispyhilitica*), the development of transportation routes and irrigation systems and, more recently, a partly subsidized resettlement program in interior valleys and exploration for petroleum (Morafka et al., 1981).

Irrigation and plowing of desert-grasslands appears to have extirpated tortoises at the southwest edge of their distribution near Tlahualilo, Yermo, and Ceballos, all in Durango. Continued human predation on adult tortoises and, to a much lesser extent on eggs, appears to be a problem throughout the range. Livestock competes for forage and may trample young tortoises.

Interviews with long-time rural residents often yield accounts of deteriorating tortoise populations, even since 1900. Tenneson (1985) interviewed a 50-year-old resident of Ejido la Flor, Durango. He estimated that tortoise populations were currently one-fourth or one-fifth the density his father had seen in the same region 60 years ago. He also remembered bringing ox carts full of tortoises to local markets. One of us (McCoy) interviewed older residents at ranchos and ejidos near Yermo and Ceballos, Durango (see Part I). These informants, men in their 70s and 80s who had lived in the area their entire lives, all related similar scenarios of tortoise population decline. A common element of these histories was that tortoises formerly (50 to 75 or more years ago) were much more abundant, although the limits of distribution were roughly the same. The initial decline in tortoise abundance was invariably attributed to a major change in demography of the local human population: influx of construction workers during the building of Highway 45, the presence of large numbers of mule teamsters during the initial leveling of land destined for irrigation, or the settling of immigrant workers in newly-opened agricultural areas. In each case it was related that hunting pressure on the tortoises was relaxed only when populations became so depleted and individuals so scattered that organized hunts were unlikely to meet with success.

Recently, the impact of PEMEX (National Petroleum Trust of Mexico) exploration roads has been expanding. These dirt strips have been bulldozed across virtually every valley in the Bolson de Mapimi in Durango, southeastern Chihuahua, and to a lesser extent, in western Coahuila. These road building operations have accelerated dramatically since 1977. These roads are unwavering, straight, and totally remove all vegetation in their path. Some capture and reorient local drainages. In March 1982, we discovered roadside campfire sites at Rancho Peñoles, Chihuahua, in which were strewn freshly shattered tortoise shells. The long-term effects of these roads are unknown but at a minimum they generate local losses of adult tortoises due to easier access. At worst, the new roads precede waves of new long-term human colonization, manifest in PEMEX drilling crews, new ejido (cooperative farm) settlements, and drives of livestock into new forage lands.

CONCLUSION

Gopherus flavomarginatus is limited geographically and populations are now fragmented. Major topographical features (mountains and playas) account for only a portion of these fragments and limits. Our field data indicate that ecological variables fail to discriminate between sites with and without tortoises. Contiguous and accessible valleys extralimital to the tortoise appear to be nearly identical in their ecological and climatic aspects to localities within the range of the species. While further comparative studies of these peripheral valleys may lead to better

habitat discrimination, our studies point to no environmental factor or set of factors that explain the existing distribution, other than human activities and human settlements. The current range boundaries of the species appear to be a collapsed shadow of the former range, confined to a few remote valleys within the Mapimian Subprovince of the Chihuahuan Desert.

The genus *Gopherus* has the best fossil record of any extant genus of North American reptile. It provides a history of waning distributions beginning in early Miocene times. Early expansions were probably associated with increases in semi-arid grasslands. *Gopherus flavomarginatus* may have become the endemic species of the Mexican Plateau as a result of renewed basin and range development of Trans-Pecos Texas and the Sierra Madre Oriental in late Pliocene times. During the late Pliocene its range may have reached a maximum as grasslands and savannas (*Yucca*, oak, and piñon-juniper) expanded into Arizona and New Mexico. Early Pleistocene uplifts of the Saladan region of the southern Mexican Plateau may have truncated the southern aspect of its range, restricting the tortoise to lower, more western river valleys or possibly isolating entirely the southernmost (late Pleistocene) populations. A single uncertain record for Aguascalientes may extend its presence in the south to Rancholabrean times (500,000 to 180,000 years BP). Subsequent glacio-pluvial lakes and marshes may have also limited tortoises in the south (Parras and Aguascalientes) and east (Llano del Guaje). Cold winters caused a southward retreat from Texas and New Mexico by the beginning of the Holocene Epoch.

End-Pleistocene and early Holocene events induced not only a massive (80%) restriction of the remaining Pleistocene range of *G. flavomarginatus*, but also the sudden mass extinction of many large terrestrial vertebrates in the Western Hemisphere. While a variety of hypotheses have been proposed, only extreme cold winters ("blue northers") and human predation are probable causal agents. The climatic and vegetation changes of the Holocene were probably a repetition of sequences that took place in preceding and occasionally more extreme interglacials. Yet past episodes induced only regional extirpations and dispersals, not mass extinctions. Furthermore, south of the 30th parallel Holocene climatic changes were less extreme, and colder winters were much less pronounced than to the north. Human invasion and expansion in North America appears to be the best documented event that distinguishes the early Holocene from preceding interglacials. Both past and present human hunter-gatherers have been devastating as predators. Turtles and tortoises are documented as food species in both Holocene and historical times. *Gopherus flavomarginatus* might have recovered its lost distribution (at least in Mapimian and Trans-Pecos subprovinces) in middle to late Holocene times had not unremitting human predation kept it in retreat, though continued and increasing "northers" may have also exercised considerable influence.

The tortoise's continued, if limited, survival is probably due to the shelter of its extensive burrow and inaccessibility of the Mapimian valleys (not connected to any major river system) in which it continues to occur. The Mapimi region probably was not as impacted by the mainstream of Paleo-Indian hunters. No archaeological evidence of riparian agricultural communities, for example, has been reported for Mapimi. Relatively infrequent northern winter storms may have helped maintain the equability of climate and diversity and productivity of Mapimian grasslands. Pluvial lake formation may have reduced the vulnerability of shoreline populations (to aboriginal hunters) until relatively late Holocene

times. The absence of surface water in modern, dry bolsons (except immediately after summer storms) may have discouraged recent Pre-Columbian human occupation.

Currently, direct and indirect human pressure continues. Within the last century, approximately 35–50% of the remaining Post-Columbian range of the tortoise was lost, primarily due to irrigation and agriculture in the south (near Torreón, Coahuila) and west (Ceballos, Durango), and continued predation everywhere (especially along major rail and road routes). Within the remaining habitats, population densities continue to be reduced in 80% of examined localities.

Several powerful and contradictory Mexican social trends make a prognosis for the tortoise's survival difficult. Casanova (1980) documented a series of 20th Century socioeconomic patterns that could endanger the quality and stability of Mexican living standards. Between 1900 and 1970 the Mexican population doubled twice, the second time in only 20 years. It reached 80 million people in 1980. Projections for the year 2000 range from 100 to 132 million persons. Economic and distributional factors may either ameliorate or exacerbate population pressure in rural areas. If industrial growth and resulting population migration to urban centers continue to draw off rural populations, net rural densities might actually drop by the year 2000. The rural share of the Mexican population dropped by half (65 to 35%) between 1940 and 1978. If it decreased by another fourth in the next 20 years (1980–2000), the net absolute increase in rural numbers could be less than 10%.

However, cultivation of arable land might undergo an increase independent of rural population growth. The national highway system increased twenty-fold between 1940 and 1977, reaching 200,000 km. Mechanized farming, tapping aquifers, and expanded distribution of ejidos in the Bolson de Mapimi all threaten tortoise populations, regardless of general population trends. Casanova estimated that more than half the population (40 million) had a nutritionally inadequate diet. In arid, rural Mexico, high living costs and inadequate diets might force the population from livestock ranching into episodic hunting and gathering. Such a shift would obviously intensify predation on the tortoise. It might threaten the voluntary program protecting tortoises at the Mapimi Reserve, which has the largest known population.

The reproductive capacity of *G. flavomarginatus* populations is not completely known. G. Aguirre (personal communication) considered clutch size (5.2), frequency (2/yr), survivorship (1 to 5%) and slow maturation time (15–20 yr) in calculating a replacement period of 25–80 yr for a reproducing adult in a colony. Grossly similar estimates for *G. polyphemus* have been made by Auffenberg and Franz (1982). The problem is compounded by our ignorance about reproductive success in scattered (non-colonial) or depleted tortoise populations. We simply do not know whether these low density populations are viable. Perhaps they are composed entirely of non-reproductive adults, isolated survivors.

Some positive events, equally uncertain in their future momentum, have been established. Community cooperation has been protecting tortoises at the MAB Mapimi Reserve since 1978 and continues to expand (G. Aguirre, personal communication, 1987). The World Wildlife Fund assisted Mexico's National Instituto de Ecologia in establishing a successful tortoise hatchery in 1983. In 1984, a new tortoise nursery was added to the Instituto Laboratory at Mapimi and it is now fully operational. However, the linked problems of nutrition, growth, and "knobby shell" formation in nursery-raised hatchlings has not yet been overcome, and the

results of the first hatchling reintroductions into natural but ungrazed enclosures remain to be recorded (Adest et al., in press).

In the Sierra del Diablo District of Chihuahua, Ing. Jose Treviño of the Mexican Sub-Secretariat for Urban Development and Ecology (SEDUE) is undertaking a detailed survey of local populations and coordinating a voluntary protection program by local ranchers. Initial results in 1983–84 are encouraging. A second hatchery and nursery has been established at Rancho Sombrerete, Chihuahua. Also, Ing. Treviño has proposed that the Sierra del Diablo be set aside as a national wildlife refuge. The refuge would include the tortoise populations east of the Sierra (Cerros Emilio, Chihuahua), nearby relict piñon woodlands, and distinctive sand dunes to the south. Organized protection of such a large tract of land, especially when combined with the MAB Mapimi Reserve, would provide a unified conservation program for the Bolson de Mapimi. In the smaller districts at Remedios, Americanos, Yermo, and Diana, conditions continue to deteriorate in absence of any corrective measures. In particular, tortoise populations near Yermo and Diana in Durango may be lost by the end of this century or sooner.

The future welfare of the resident Mexicans and their Bolson tortoise are indivisible. Just as the Holocene collapse of tortoise distribution depended largely upon human conduct, so is its continued survival today. No written political policy will dictate the actions of ranchers and ejido inhabitants. Only the well being, consciousness, and personal values of local Mexicans shall decide whether *G. flavomarginatus* is to become just another late addition to the list of megafauna casualties or whether it will be nurtured and sustained as the centerpiece of the Mapimian desert-grassland which is unique to Mexico's natural heritage.

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A PHYLOGENETIC ANALYSIS OF POSTCRANIAL SKELETAL CHARACTERS OF THE RATITE BIRDS

ANTHONY H. BLEDSE¹

Rea Postdoctoral Fellow and Research Associate, Section of Birds

ABSTRACT

A numerical cladistic analysis of 83 skeletal characters of the ratite birds produced a minimum-length tree in which: the ostriches (*Struthio*) and rheas (*Rhea*) form the sister group of the elephant-birds (*Aepyornis*); the cassowaries (*Casuarius*) and emus (*Dromaius*) are the sister group of the kiwis (*Apteryx*); and the *Struthio-Rhea-Aepyornis* and *Casuarius-Dromaius-Apteryx* clades are sister groups, together forming the sister group of the moas (*Dinornithidae*). The positions of the moas and elephant-birds varied among longer alternative topologies, in part because many of their character states are not known. In contrast, the pattern of branching among the extant ratites was insensitive to small increases in tree length and broadly congruent with the results of molecular comparisons.

INTRODUCTION

Although the living species of ostriches, rheas, cassowaries, emus and kiwis were described over 100 years ago, are few in number, and have been studied in considerable detail, avian systematists have been unable to reach a consensus about their phylogenetic relationships. The wide interest in flightless paleognaths and the regularity with which systematists have commented on them, however, belie the lack of adequate studies of the degree to which various sets of characters support alternative phylogenetic reconstructions. For instance, since Merrem (1813) united the large ratites because they lack keeled sterna, systematists have frequently invoked osteological characters to support their phylogenetic contentions, with important contributions by Huxley (1867), Mivart (1877), Fürbringer (1888, 1902), Pycraft (1900), McDowell (1948), Zavattari and Cellini (1956), Bock (1963), Cracraft (1974, 1987), and Rich (1979). However, despite the large amount of information produced by these studies, the osteological variation among the ostriches, rheas, cassowaries, emus and kiwis has not been rigorously analyzed.

Cracraft (1974), in an effort to provide such an analysis, studied the taxonomic distribution of 25 postcranial osteological characters. However, the set of characters employed by Cracraft contained virtually no homoplasy, a surprising result given that sets of postcranial skeletal characters in other groups (e.g., Alcidae, Strauch, 1985; Pelecaniformes, Cracraft, 1985) typically exhibit high levels of parallelism and reversal. In 1980, I began comparisons of ratite skeletons and observed additional characters not noted by Cracraft (1974), as well as variation that made it difficult to determine the ancestral state of several characters he employed. Subsequently, I became aware that a monograph by Rich (1979) on the *Dromornithidae*, a family of flightless birds known from fossils from the Miocene to Pleistocene of Australia, provided a large compilation of postcranial skeletal characters of the ratites. Rich's analysis included the characters I had observed and several others as well, and excluded the problematic characters used

¹ Current address: Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260. Submitted 29 April 1987.

by Cracraft. It became evident that Rich's compilation included most of the useful characters of the postcranial skeletons of the living and recently extinct ratites.

This paper presents a phylogenetic analysis of Rich's (1979) characters. The goal of the analysis was to estimate the phylogeny of the ratites with numerical cladistic methods, using a larger set of characters than that used by Cracraft (1974). I then compared the results of the cladistic analysis with those obtained from molecular and other morphological studies of the ratite birds.

I assumed initially that the ostriches (*Struthio*), rheas (*Rhea*), elephant-birds (*Aepyornis*), cassowaries (*Casuarius*), emus (*Dromaius*), kiwis (*Apteryx*) and moas (*Dinornithidae*): (1) are derived from flying birds; and (2) form a monophyletic group (termed the ratites) that is the sister group of the tinamous (*Tinamidae*). Although some workers (e.g., McGowan, 1986) continue to maintain that none of the ancestors of the ratites was volant, most avian systematists accept the derivation of the ratites from flying ancestors because the anatomical evidence for such a derivation (DeBeer, 1956) is extensive. The hypothesis of monophyly, however, remains controversial. The results of molecular (Prager et al., 1976; Sibley and Ahlquist in Diamond, 1983; Stapel et al., 1984), behavioral (Meise, 1963) and morphological (Parkes and Clark, 1966; Cracraft, 1987) studies support the monophyly of the ratites and a sister-group relationship between them and the tinamous. The initial assumption of monophyly thus rests on the congruence of these lines of evidence.

TAXA, CHARACTERS AND CLADISTIC METHODS

Taxa.—The following taxa formed the operational units for the cladistic analysis: *Tinamidae*, *Struthio*, *Rhea*, *Apteryx*, *Casuarius*, *Dromaius*, *Aepyornis*, *Dinornithidae* and *Dromornithidae*. I assumed that *Apteryx* (three species, Mayr, 1979), *Casuarius* (three species, Mayr, 1979), *Dromaius* (two species, Mayr, 1979), and the *Dinornithidae* (*sensu* Cracraft, 1976) are each monophyletic (see Appendix for a list of the species examined). *Struthio* and *Rhea* (*sensu* Mayr, 1979) are monotypic, as *Aepyornis* is also considered here. Neither I nor Rich (1979) examined specimens of the Lesser Rhea (*Pterocnemia pennata*), and *Pterocnemia* was not included in the analysis. (See the section on cladistic analysis for a discussion of the treatment of the *Dromornithidae*, which may not be ratites.)

Characters.—I compared skeletal specimens of ratites, tinamous and selected species of Galliformes and Anseriformes to define the characters and character states for cladistic analysis (see Appendix for description of the characters and a list of examined specimens). The distribution of character states among ratite taxa is tabulated in Table 1 in the Appendix. In most instances, the definitions were similar to those of Rich (1979). I excluded characters that were highly variable within a taxon (e.g., length of the costal margin of the sternum in *Apteryx*) or difficult to define unambiguously. The anatomical nomenclature of Baumel et al. (1979) is used throughout.

Cladistic analysis.—Character states were coded for the numerical cladistic analysis. The ancestral state of each character was considered to be the state found uniformly among tinamous and also present in other carinate birds (e.g., Galliformes). This particular "outgroup" method relies on the initial assumptions discussed above. Because the evolutionary transformations between multiple derived states of a single character are not known, I did not impose *a priori* assumptions of transformation between such states. For characters with a single derived state, the ancestral state was coded "0" and the derived state "1." Each

character with multiple derived states was divided into several characters, one for each derived state (see Table 2 in the Appendix). With this method, clades were based on evident synapomorphy rather than synapomorphy presumed from transformations for which there is no evidence. I performed a second analysis using a different method of coding characters with more than one derived state. The ancestral state was designated "0" and each derived state was coded with a separate number (e.g., "1," "2," "3"). The transformation series requiring the fewest steps were then found using the UNORDERED option of the computer program PAUP (see below). For both methods of coding, characters that varied within an operational taxonomic unit and the character states not known in the Dinornithidae and Aepyornithidae were coded as "unknown," which for the purposes of numerical cladistic analysis was interpreted as "any possible state."

The coded character states were analyzed with the computer program PAUP (Phylogenetic Analysis using Parsimony, version 2.4, by D. L. Swofford), using the ALLTREES option and Farris' (1970) method of assigning character states to internal nodes. The ALLTREES option seeks the shortest tree among all possible topologies for nine or fewer taxa. (See Cracraft, 1985 for a discussion of numerical cladistics.) The shortest tree was rooted at a hypothetical ancestor with the ancestral state for all characters.

The idea of the minimum-length criterion (often equated with "parsimony") is that it requires the fewest *ad hoc* hypotheses and provides an objective basis for choosing among several hypotheses. A minimum-length tree has minimum homoplasy (parallel and reverse character-state changes) and maximum character congruence (Cracraft, 1985). Thus, although the evolution of characters might in reality be more complex than implied by the minimum-length criterion, the choice among trees is based on the simplest hypothesis for which evidence is available.

The consistency index (CI) is a measure of the amount of homoplasy and was calculated for each tree and for the sets of character states delimiting each group of taxa ($CI = \text{the minimum number of possible character-state changes divided by the actual number of character-state changes}$). I ignored autapomorphic characters in calculating CI and tree lengths to avoid inflating CI values artificially.

To determine how stable clades were under different character-state distributions, the BANDB option of PAUP was used to construct trees that were several steps longer than the shortest tree. The CONTREE program of PAUP was used to produce strict (Rohlf, 1982) and Adams (1972) consensus trees from the set of slightly longer phylogenies.

The Dromornithidae were not included in the main cladistic analysis because the palatal and rhamphothecal evidence for their inclusion with the ratites is fragmentary (Olson 1985). I included the Dromornithidae with the other taxa in a separate cladistic analysis.

RESULTS

Fig. 1 depicts the minimum-length tree (length = 130, CI = 0.61) and character-state distribution based on the method of coding that treated each derived state as a separate character (see "Taxa, Characters and Cladistic Methods"). Of 79 non-autapomorphic derived character states, 36 (46%) were derived only once, 24 (30%) were independently derived twice, 11 (14%) were derived once and lost once, seven (9%) were derived once and lost independently twice, and one (1%) was independently derived twice and lost once. In five instances, the loss of a derived state was associated with a gain of another derived state of the same

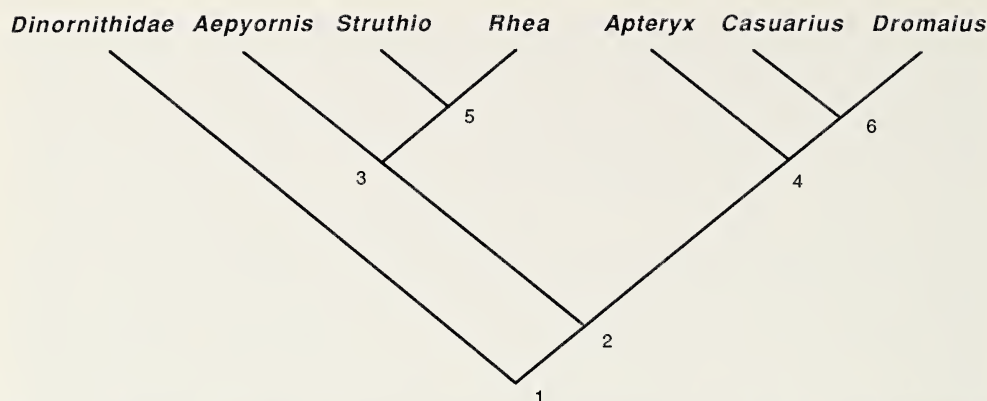


Fig. 1.—Phylogeny of the ratite birds estimated from numerical cladistic analysis of postcranial skeletal characters. The tree is rooted to a hypothetical ancestor (not shown) with the ancestral state for all characters, which corresponds to the Tinamidae (see text). The character-state changes (including autapomorphies) are listed below for the non-terminal clades (designated by numbers next to the nodes of the tree) and for the terminal taxa. Unless otherwise indicated, changes are from the ancestral condition (a) to the listed derived state. See Appendix for characters and character states. *Clade 1*: 5d, 6b, 12b, 13b, 18b, 28b, 29b, 33b, 46b, 52b, 63b, 67c, 68b, 71b, 72b, 78b. *Clade 2*: 2c, 35b, 49b, 57b, 69b, 70b, 73b. *Clade 3*: 7b, 8b, 9b, 19b, 21c, 22b, 51c, 53b, 59b, 60b, 64c, 72b. *Clade 4*: 19c, 26b, 30c, 31b, 32b, 34b, 44b, 48b, 56b, 64b, 71b→a. *Clade 5*: 5d→c, 11b, 14c, 15b, 37c, 38b, 42b, 43b, 45b, 46b→c, 47c, 50c, 52b→c, 61b, 62c, 66c, 68b→a. *Clade 6*: 3c, 4b, 5d→c, 6b→a, 13b→a, 14b, 18b→a, 21b, 22c, 27b, 37b, 38c, 40c, 41b, 45b, 47c, 50b, 52b→c, 53c, 54b, 55b, 66c, 70b→c, 74b. *Dinornithidae*: 3b, 38b, 43b, 65b, 76b, 80b. *Aepyornis*: 1c, 11c, 14b, 15c, 27b, 35b→a, 37b, 38b, 40c, 44c, 49b→a, 54b, 55b, 62b, 65b, 66c, 72c. *Struthio*: 3c, 4c, 6b→a, 19b→a, 28b→a, 39b, 44d, 75b, 79c, 80b, 82b. *Rhea*: 2c→a, 4b, 5b, 8b→a, 41b, 44b, 48b, 59b→a, 71b→a, 74b, 80c. *Apteryx*: 1b, 2c→a, 9c, 14c, 16b, 21d, 22d, 24b, 25b, 40b, 43c, 46b→a, 47b, 73b→a, 80d. *Casuarius*: 11c, 28b→a, 30c→b. *Dromaius*: 8b, 11d, 15b.

character, constituting evidence for a linear transformation series (5d→c→b, 30c→b, 46b→c, 52b→c, and 70b→c).

The descriptions of the character suites below are based on Fig. 1.

All Ratites

Sixteen derived character states delimit this clade, of which six showed no homoplasy, four were lost once, and six were lost twice (CI = 0.62).

The ventral surface of the sternum is flattened (5d) and its articular coracoidal sulci are restricted to the lateral margins (6b). On the humerus, the transverse ligamental sulcus is shallow (12b), the pneumatic foramen is lacking (13b), and a ridge is present at the base of the pectoral crest (18b). The radius is broad (28b), the ulna and radius are longer than the humerus (29b), and os metacarpale majus is compressed dorsoventrally (33b). The lateral condyle of the femur is elongated (46b). On the tibiotarsus, the articular surface of the head is expanded (52b), and the lateral epicondylar depression is deep (63b). On the tarsometatarsus, only one hypotarsal sulcus is present (67c), the hypotarsus is shifted toward the midline of the shaft (68b), the depression between the hypotarsus and intercotylar area is absent (71b), the medial cotyla is enlarged (72b), and the margins of trochlea III are straightened (78b).

The conditions of several character states coded as unknown are hypothesized to be derived in the *Dinornithidae* (12b, 18b, 28b, 29b, 33b, 78b) and *Aepyornis* (28b, 33b), based on the PAUP analysis.

All Taxa but Dinornithidae

The Dinornithidae form the sister group of the other ratites, which are delimited by seven derived character states, of which two showed no homoplasy, four were lost once, and one was lost twice (CI = 0.54).

The craniolateral process of the sternum is very short (2c), the synsacrum is narrow (35b), the muscle impression near the popliteal fossa of the femur is reduced (49b), and the supratendinal bridge of the tibiotarsus is lacking (57b). On the tarsometatarsus, the medial margin of the medial condyle is smooth (69b), the hypotarsus is expanded distally (70b), and the number of subhypotarsal ridges is reduced to one (73b).

In *Aepyornis*, the condition of one character state coded as missing is hypothesized to be derived (70b), based on the PAUP analysis.

Aepyornis-Struthio-Rhea

This clade is delimited by 12 derived states, of which eight exhibited no homoplasy, three were subsequently lost once in this clade, and one was lost once in this clade and independently evolved once elsewhere in the tree (CI = 0.71).

The glenoid facet of the scapulocoracoid is shifted dorsally (7b), a groove medial of the glenoid cavity is present (8b), and the surface between the cranial surface of the glenoid cavity and the medial margin of the scapulocoracoid is knob-like (9b). On the humerus, the dorsal epicondyle is reduced (19b), the shaft is triangular in cross-section (21c), and the distal end is widened caudally (22b). On the tibiotarsus, the cnemial crests are substantially compressed (51c), the cranial cnemial crest is shortened (53b), the ridge extending laterally from the extensor canal is lacking (59b), the craniodistal edge of the lateral condyle is elliptical (60b), and the medial condyle is very wide and very short (64c). The medial condyle of the tarsometatarsus is enlarged (72b).

In *Aepyornis*, the conditions of three character states coded as missing are hypothesized to be derived (7b, 21c, 22b), based on the PAUP analysis.

Struthio-Rhea

This clade forms the sister group of *Aepyornis* and is delimited by 15 derived states (seven with no homoplasy and eight evolved independently elsewhere in the tree), two of which were acquired by concomitant loss of a separate derived state for the same character, and by two reacquired ancestral states (CI = 0.56).

The ventral surface of the sternum is curved (5d→c). The humerus is slender and elongate (11b), its ventral tuberculum is expanded (14c), and the head is shifted dorsally away from the dorsoventral midline (15b). On the synsacrum, the trochanter is shifted cranially (37c) and the pubis is elongated relative to the ilium and ischium (38b) and is widened (42b). On the femur, the caudal margin of the antitrochanteric articular surface is straightened (43b), the axes of the medial and lateral condyles are divergent (45b), the lateral condyle is even further elongated distally (46b→c), the cranial margin of the lateral condyle is highly concave (47c), and the distal margin of the medial condyle is flattened (50c). On the tibiotarsus, the cranial cnemial crest is expanded relative to the rest of the articular surface (52b→c), the cranial-most extension of the lateral condyle lies proximal of the condyle's proximodistal midpoint (61b), and the lateral condyle is extended caudally (62c). The hypotarsus of the tarsometatarsus is formed into a narrow ridge (66c) and is shifted toward the proximodistal midline of the shaft's axis (68b→a).

Casuarius-Dromaius-Apteryx

This clade forms the sister group of the *Aepyornis-Struthio-Rhea* lineage and is delimited by ten derived states, including seven with no homoplasy, two independently gained once elsewhere in the tree, and one lost once in this clade, and by a single reacquired ancestral state (CI = 0.69).

The dorsal epicondyle of the humerus is highly reduced (19c). On the ulna and radius, the proximal end is narrowed (26b), the carpal trochlea is flattened (30c), the phalangeal articulation of os metacarpale alulare is lacking (31b), os metacarpale majus and minus are fused completely (32b), and only one metacarpal has a phalangeal articulation (34b). The trochanteric crest of the femur is shortened (44b), as is the fibular trochlea (48b). On the tibiotarsus, the intercondylar eminence is lacking (56b), and the medial condyle is shortened (64b). The depression between the intercotylar area and the hypotarsus of the tarsometatarsus is present (71b→a).

Casuarius-Dromaius

This clade, the sister group of *Apteryx*, is delimited by 21 derived states, including six with no homoplasy and 15 acquired independently elsewhere in the tree, and by six reacquired ancestral states, three of which were re-evolved only in this clade, and three of which were also re-evolved elsewhere in the tree (CI = 0.53).

On the sternum, the cranial margin is convex (3c), the incisures are lacking (4b), the ventral surface is curved (5d→c), and the articular coracoidal sulci is located medially (6b→a). On the humerus, a pneumatic foramen is present (13b→a), the ventral tuberculum is lengthened (14b), the ridge at the base of the pectoral crest is absent (18b→a), the shaft is circular in cross-section (21b), and the margins of the distal end are straightened (22c). The ulna and radius are fused (27b). On the synsacrum, the trochanter is shifted cranially (37b), the pubis, ilium and ischium are nearly equal in caudal extension (38c), the postacetabular ilium is widened (40c), and the preacetabular tuberculum is shortened (41b). On the femur, the margins of the medial and lateral condyles are tilted relative to the shaft (45b), the lateral condyle is highly concave cranially (47c), and the distal margin of the medial condyle is slightly flattened (50b). On the tibiotarsus, the cranial cnemial crest is expanded (52b→c) and extended (53c), the lateral margin of the proximal end is deeply concave (54b), and the channels at the margins of the intercondylar eminence are absent (55b). On the tibiotarsus, the hypotarsus is formed into a narrow ridge (66c) and extends beyond the intercotylar area (70b→c), and the plantar surface is deeply grooved (74b).

The condition of one character state (27b) coded as unknown (polymorphic) in *Casuarius* is considered to be derived, based on the PAUP analysis.

Alternative Trees

There were 16 trees longer than the shortest tree by 1–3 steps (lengths 131–133). One tree united the cassowary-emu and rhea-ostrich clades as sister groups, forming the sister group of the kiwis, with the moas and elephant-birds forming a clade and the sister group of the other ratites. The remaining 15 topologies differed from the tree in Fig. 1 only in the positions of elephant-birds and moas. Of these, five united the moas and elephant-birds as sister groups, this clade being the sister group either of the ostriches and rheas, of the cassowary-emu-kiwi

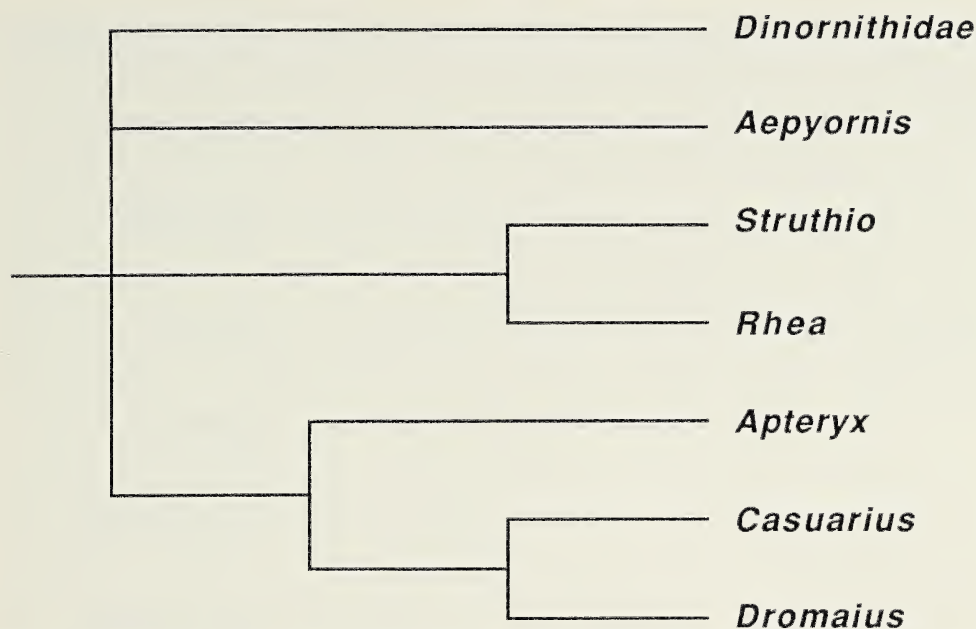


Fig. 2.—Consensus tree constructed from the set of alternative trees (see text) using the method of Adams (1972) for trees with unlabeled internal nodes. This method seeks the intersection of the inclusive sets of the alternative trees.

lineage, of the cassowaries and emus, of the kiwis, or of all of the other living ratites. Four trees placed the elephant-birds as the sister group of the cassowaries and emus; in these, the moas were the sister group either of the kiwis, of the cassowary-emu-*Aepyornis* clade, of the lineage including the kiwis, emus, cassowaries and elephant-birds, or of all of the other ratites. Of the other remaining six alternatives, one was identical to Fig. 1 in topology but not in character-state distribution, while three were identical to Fig. 1 except in the position of the moas, which were the sister group either of the ostriches and rheas, of the ostrich-rhea-*Aepyornis* clade, or of the Australo-New Zealand ratites. In one tree, the moas were the sister group of the kiwi-cassowary-emu clade, forming an assemblage that was the sister group of the elephant-birds, while in another these positions of the elephant-birds and moas were reversed. Fig. 2 and 3 present consensus phylogenies based on the set of trees of length 130–133.

Analysis of the data set based on the alternative method of coding produced a tree identical in topology to Fig. 1 except in placing the elephant-birds as the sister group of the cassowary-emu lineage (length = 137, CI = 0.68).

Analysis Including the Dromornithidae

This analysis produced a tree that for the living ratites was identical in topology to Fig. 1 but that placed the mihirung-birds as the sister group of the cassowary-emu lineage, the elephant-birds as the sister group of the cassowary-emu-Dromornithidae clade, and the moas as the next successive sister group (length = 162, CI = 0.54). The pattern of character states changed when the mihirung-birds were included. In the suite of states uniting the ratites, the Dromornithidae ex-

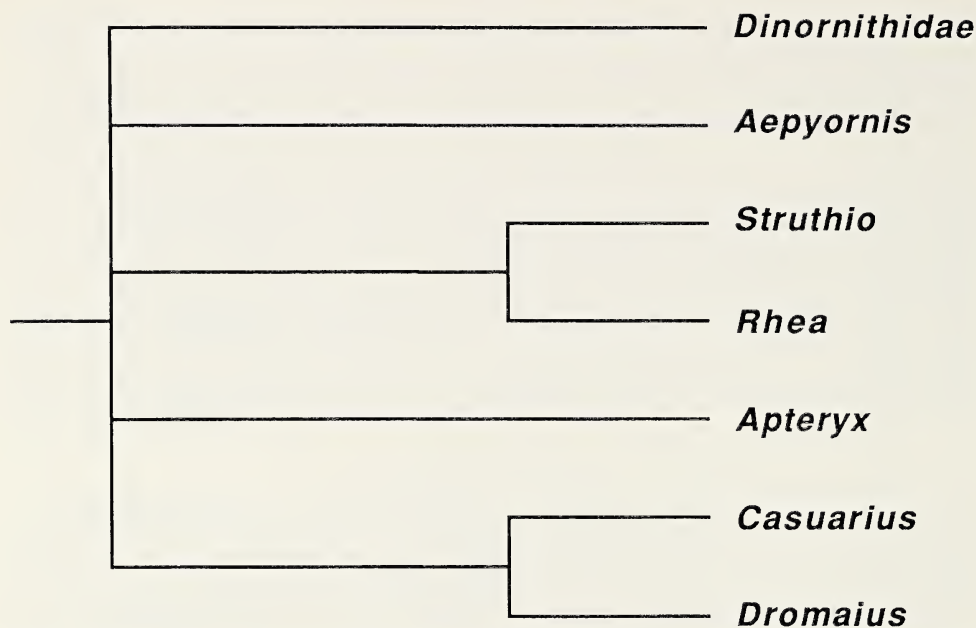


Fig. 3.—Consensus tree constructed from the set of alternative trees (see text) using the method of Rohlf (1982). This method produces a “strict” consensus tree including only the identical sets of taxa among the alternative trees.

hibited none of the six non-homoplastic derived states in the analysis excluding the Dromornithidae.

DISCUSSION

The phylogenies in Fig. 1–3 corroborate the initial hypothesis of monophyly of the ratites and add to the behavioral (Meise, 1963), molecular (Prager et al., 1976; Sibley and Ahlquist *in* Diamond, 1983), and morphological (Mivart, 1877; Cracraft, 1974, 1987) data in support of ratite monophyly. The pattern of branching among the living ratites was essentially stable as tree length increased, being the same as in Fig. 1 in 15 of 16 alternative trees and in the analysis employing an alternate method of character-coding. The results of the numerical cladistic analysis thus also supplement the substantial body of evidence supporting the monophyly of the ostriches and rheas (Mivart, 1877; Meise, 1963; Cracraft, 1974; Sibley and Ahlquist *in* Diamond, 1983), and of the cassowaries and emus (Mivart, 1877; Meise, 1963; Cracraft, 1974; Prager et al., 1976; Sibley and Ahlquist *in* Diamond, 1983).

The clade consisting of the cassowaries, emus, and kiwis has also been proposed previously on morphological (Mivart, 1877) and biochemical (Sibley and Ahlquist *in* Diamond, 1983) grounds. However, the cassowary-emu-kiwi clade is at odds in two respects with Cracraft's (1974) analysis. First, Cracraft surmised that the cassowaries and emus are the sister group of the ostriches and rheas. Second, like nearly all previous workers, Cracraft allied the kiwis with the moas rather than with the Australian-New Guinea ratites.

The discrepancies between the views of Cracraft (1974) and the phylogeny in Fig. 1 are probably best explained by differences in the size of the data sets and

the extent of the comparisons. Cracraft used a smaller set of characters (25) that did not encompass the taxonomic variation of the forelimb elements. In addition, several of the characters he used were not included here because they vary among Tinamidae and other outgroup taxa. For instance, cassowaries, emus, ostriches, rheas and elephant-birds possess a long, deep cranial metatarsal groove, but some tinamou specimens (e.g., *Tinamus major*, AMNH 3675; *Crypturellus noctivagus*, AMNH 10443) exhibit the same condition, so that its apomorphy is uncertain. For other characters, Cracraft's assessment of taxonomic occurrence was incomplete. For example, Cracraft used (among other characters) the loss of the supratendinal bridge in cassowaries, emus, ostriches, rheas and elephant-birds to unite them, yet the kiwis lack a supratendinal bridge as well. That Cracraft identified only a single homoplastic character, the width of the pelvis, when homoplasy is so extensive in the data set analyzed here, suggests that Cracraft's comparisons were less detailed than those used in the present study.

Thus, the phylogeny in Fig. 1 is more informative and probably a better estimate of phylogeny than Cracraft's (1974) arrangement. His analysis nonetheless showed that nearly all previous workers failed to consider the plesiomorphy and apomorphy of characters. This is particularly true for characters traditionally used (e.g., Oliver, 1949) to ally the moas and kiwis, as Cracraft (1974) noted. Cracraft (1974) observed four derived character states allying the moas and kiwis, of which three were not used in the current study. The projection of trochlea III distally beyond trochleae II and IV occurs in some tinamids, as Cracraft noted, and its apomorphy is thus unclear. The location of the coracoid process of the scapulocoracoid adjacent to the glenoid cavity is indeed shared only among moas and kiwis, but its ancestral state is difficult to infer because no strictly comparable character occurs among the outgroups. The presence of a single deep hypotarsal sulcus hinges on the apomorphy of the number of sulci rather than their depth, because the ancestral condition is for each sulcus to be deep. The other ratites possess a single sulcus (67c), although the Dromornithidae have two sulci (67b). A fourth character used by Cracraft to ally the moas and kiwis—the relative projections of the medial and lateral condyles of the tibiotarsus—is defined somewhat differently in this study (character 65) and as a result *Apteryx* shows the ancestral state while the moas and elephant-birds possess the derived condition. However, even if Cracraft's definition of this character is admitted in place of character 65, the topology of Fig. 1 is not altered.

Thus, the results of this study support Cracraft's contention (1974) that it is difficult to recognize characters confirming the monophyly of the moas and kiwis. However, even though the moas and kiwis are not sister groups in Fig. 1 nor in 15 of 16 alternative trees, the absence of wings from moas might compromise the ability to infer the frequently proposed sister-group relationship between moas and kiwis (and the one with the simplest biogeographic interpretation) even if that arrangement were indeed correct. Wing bones of moas have never been found (Oliver, 1949), and the absence of a glenoid facet on the scapulocoracoid indicates that the moas probably lacked them.

An analogous situation applies to the elephant-birds, for which 12 character states are not known because several of the wing elements are poorly preserved. The lack of such information does not weaken the conclusion of ratite monophyly because the extinct taxa exhibit other character states delimiting the ratites (Fig. 1), as well as the rhamphothecal structure described by Parkes and Clark (1966) and the derived palatal characters discussed by Cracraft (1987). However, because

the PAUP program allows missing character states to vary among all possible conditions, the lack of knowledge of many character states in the moas and elephant-birds creates a situation in which these taxa may assume almost any position on an otherwise stable tree. Thus, additional information will be required to determine if Fig. 1 provides a good estimate of the relationships of the moas and elephant-birds.

The relationships of the extinct mihirung-birds (Dromornithidae) of Australia are even more difficult to infer. Their possession of the ancestral state of the six non-homoplastic character states delimiting the ratite clade is consistent with the hypothesis that they are not members of that clade, but they share the derived state of several other characters with the ratites. The remains of the palate and rhamphotheca of the mihirung-birds are so fragmentary and poorly preserved (see Olson, 1985:104–105) that they do not clarify the situation. The phylogenetic relationships of the mihirung-birds are thus not resolved by this study.

Since Cracraft's study, several analyses of ratite phylogeny have been published. Some (e.g., Feduccia, 1980:133; Olson, 1985) were based on a few, incompletely surveyed morphological characters of uncertain apomorphy, and on the idea that differences argue against monophyly of taxa. For instance, Olson (1985:102) stated that "the great diversity in . . . morphology within the large ratites favors their having evolved their ratite grade of morphology independently of one another." There is no doubt that the ratites are diverse morphologically, but without evidence of a relationship to other groups of birds (in the form of derived character states, macromolecular evidence, etc.), the hypothesis of independent evolution of the morphological similarities among the ratites receives no phylogenetic support. It makes no sense to suppose that morphological diversity alone is indicative of non-monophyly (Raikow and Cracraft, 1983).

Houde (1986) maintained that several "paleognathous" volant fossil taxa known from the Paleocene and Eocene of North America and Europe "gave rise to the various lineages of ratite birds." However, of the ratites, Houde included only the kiwis and ostriches, and like Olson (1985) and Feduccia (1980), did not present a complete character-set for the diagram of relationships he depicted. Although the phylogeny presented by Houde is fully consistent with Fig. 1, it is difficult to assess the validity of his results or of the opinions of Olson (1985) and Feduccia (1980) without a more complete study.

Rich (1979) employed a tally of shared derived states among each pairwise combination of ratite taxa to infer three possible phylogenies of the ratites. Even though the derived states she observed form the basis for the current study, each of the alternatives she proposed differs from the topology in Fig. 1 except in grouping the cassowaries with the emus and the ostriches with the rheas. The alternative she proposed on the basis of an outgroup method of determining polarity placed the moas and kiwis as sister groups, together forming the sister group of the other ratites; the elephant-birds were the sister group of a clade in which the Dromornithidae and Casuariidae formed the sister group of the ostriches and rheas. However, a PAUP analysis of the character states of the present study indicated that this topology is longer (length = 176, CI = 0.52) than the comparable tree presented here, that which included the Dromornithidae (length = 162, CI = 0.54). Thus, the "tally" method of Rich (1979) did not identify the shortest possible tree.

Prager et al. (1976) used immunological comparisons of transferrins to propose a tree linking cassowaries and emus as sister groups, with a trifurcation between

the cassowary-emu clade, the kiwis and the rheas, and another trifurcation between these taxa and the ostriches and tinamous. Although these trifurcations reduce the resolution of the tree, its topology is nonetheless consistent with that of Fig. 1, except in the position of *Rhea*, which is not the sister group of *Struthio* in the phylogeny proposed by Prager et al. (1976).

Sibley and Ahlquist (*in* Diamond 1983) used DNA-DNA hybridization comparisons to construct a tree identical to Fig. 1 in its branching pattern among the living ratites. However, the thermal dissociation curves and distances reported in an earlier study (Sibley and Ahlquist 1981, Figs. 5–10, Table 1) indicated that the ostriches and rheas are farther from each other than either is from the cassowaries, emus and kiwis. If the later phylogeny of Sibley and Ahlquist is taken as the definitive DNA phylogeny, then congruence between it and Fig. 1 would argue for the validity of both as estimates of the phylogeny of the ratites.

The most serious potential objection to the present study is that the characters are primarily qualitative and thus are difficult to partition into discrete states. Such character states also might have evolved concomitantly through neoteny and an increase in body size, which may have occurred independently in the various groups (Raikow 1985:91). The high level of homoplasy in Fig. 1, which is characteristic of avian phylogenies employing osteological traits (Strauch, 1985, Livezey, 1986), reflects an inability to recognize the nonhomology that, at some level, must exist to explain such discordant distributions among character states. Yet the suggestion of congruence between the morphological and molecular approaches implies that, in this instance, each provides a good estimate of phylogeny, and by implication that qualitative osteological characters carry substantial phylogenetic information. If this is correct, a more quantitative analysis of osteological variation should yield results congruent with the results presented here and with other lines of phylogenetic evidence, both molecular and morphological.

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APPENDIX

Specimens.—Skeletal specimens of the following taxa were compared (AMNH = American Museum of Natural History; YPM = Peabody Museum of Natural History, Yale University). Tinamidae: *Tinamus solitarius* (YPM 2085), *T. major* (AMNH 3675, 5283; YPM 374), *Crypturellus undulatus* (AMNH 6479, 6481; YPM 11564), *C. noctivagus* (AMNH 10443, 10444, 10445; YPM 2120, 2121), *Rhynchotus rufescens* (YPM 2041), *Nothoprocta perdicaria* (YPM 2040, 6696), *N. cinerascens* (AMNH 6505, 6507, 6509), *Nothura darwinii* (YPM 6697), *N. maculosa* (AMNH 2325, 2864, 3540; YPM 2086), *Eudromia elegans* (AMNH 8565, 8678, 9152, 11395; YPM 2086). Struthionidae: *Struthio camelus* (YPM 560, 561, 2116, 2117, 2124, 4236, 4347, 4382, 4799). Rheidae: *Rhea americana* (AMNH 1500, 1673; YPM 2234, 6503, 11524). Casuariidae: *Casuarius* sp. (AMNH 1517; YPM 2123, 4351, 6208), *Dromaius novaehollandiae* (YPM 567, 2127, 2128, 2129). Apterygidae: *Apteryx australis* (YPM 4383, one uncatalogued specimen), *A. owenii* (YPM 2118), *Apteryx* sp. (AMNH 3738, 3739, 4437, 5372). Dinornithidae: *Pachyornis elephantopus* (YPM Vertebrate Paleontology [VP], uncatalogued material), *Euryapteryx* sp. (YPM VP, uncatalogued material), *Dinornis "maximus"* (= *giganteus*, YPM VP 9206), *D. "gracilis"* (YPM VP 9207), *D. struthoides* (YPM VP, uncatalogued material). I also examined a large series of skeletal specimens of *Bonasa umbellus* and single specimens of selected species of Galliformes and Anseriformes for analysis of character polarity. I was unable to study specimens of the Lesser Rhea (*Pterocnemia pennata*), *Aepyornis maximus*, and the Dromornithidae. For *Aepyornis* and the Dromornithidae, I thus used the character descriptions provided by Rich (1979).

Characters.—The characters used for numerical cladistic analysis are listed and numbered below, grouped by skeletal element. The character is described first, followed by the ancestral and derived states, designated alphabetically beginning with the ancestral state (a). The alphabetical order of the character states does not imply a linear transformation series among multiple derived states of a single character. The terminology follows Baumel et al. (1979).

Sternum

1. Proportions: (a) longer (craniocaudally) than wide (mediolaterally); (b) length and width equal; (c) wider than long.
2. Craniolateral process: (a) elongate; (b) shortened; (c) very short.
3. Cranial margin: (a) concave cranially; (b) straight; (c) convex cranially.
4. Number of incisures: (a) two; (b) none; (c) four.
5. Ventral surface: (a) highly curved, carina present; (b) highly curved, low medial ridge present; (c) moderately curved, no distinct medial ridge; (d) flattened.
6. Articular coracoidal sulci: (a) meet or nearly meet medially; (b) restricted to lateral margins.

Scapulocoracoid

7. Orientation of glenoid facet: (a) lateral; (b) dorsolateral.
8. Groove medial of glenoid cavity: (a) absent; (b) present.
9. Cranial surface between glenoid cavity and medial margin: (a) smooth; (b) knobbed; (c) ridged.
10. Scapular body: (a) lateral facet concave; (b) medial facet concave.

Humerus

11. Proportions: (a) slender, length moderate; (b) slender, elongate; (c) stout, short; (d) slender, short.
12. Transverse ligamental sulcus: (a) deep; (b) shallow; (c) absent.
13. Pneumatic foramen: (a) present; (b) absent.
14. Proximal protrusion of ventral tuberculum and head: (a) head protrudes beyond tuberculum; (b) subequal; (c) tuberculum protrudes beyond head.
15. Position of head: (a) near midline; (b) shifted dorsally; (c) shifted ventrally.
16. Ligamental impression on ventral surface of shaft near its midpoint: (a) absent; (b) present.

17. Fossa of m. brachialis: (a) small, shallow; (b) large, deep.
18. Ridge at base of pectoral crest: (a) absent; (b) present.
19. Dorsal epicondyle: (a) well developed; (b) moderately developed; (c) highly reduced.
20. Articular surfaces: (a) sharply defined; (b) poorly defined.
21. Shape of shaft in cross-section: (a) elliptical proximally and distally; (b) circular proximally and distally; (c) triangular proximally and distally; (d) triangular proximally, elliptical distally.
22. Distal end: (a) widest cranially; (b) widest caudally; (c) cranial, medial and caudal widths subequal; (d) widest medially.
23. Olecranal fossa: (a) absent or very shallow; (b) well developed.

Ulna-radius

24. Proximal articular surface of ulna: (a) well developed; (b) poorly defined.
25. Olecranon: (a) large; (b) reduced.
26. Proximal end of ulna: (a) broad in proximal view; (b) narrow in proximal view.
27. Ulna and radius: (a) unfused; (b) fused.
28. Width of shafts of ulna and radius: (a) ulna broader; (b) subequal.
29. Lengths of ulna-radius and humerus: (a) subequal; (b) ulna-radius longer than humerus; (c) humerus longer than ulna-radius.
30. Carpal trochlea: (a) highly curved; (b) moderately curved; (c) flattened.
31. Phalangeal articulation on os metacarpale alulare: (a) present; (b) absent.
32. Fusion of os metacarpale majus and os metacarpale minus: (a) incomplete; (b) complete.
33. Os metacarpale majus: (a) wide dorsoventrally; (b) compressed dorsoventrally.
34. Number of metacarpals with phalangeal articulation: (a) three; (b) one.

Synsacrum

35. Dorsal surface of synsacrum caudal of the antitrochanter: (a) broad; (b) narrow.
36. Dorsal surface of synsacrum caudal of the antitrochanter: (a) decreases in width posteriorly; (b) does not narrow substantially caudally.
37. Position of trochanter (craniocaudal axis): (a) cranial of midpoint; (b) at midpoint; (c) caudal of midpoint.
38. Caudal protrusion of ilium, ischium and pubis: (a) pubis and ischium extend beyond ilium; (b) pubis extends beyond ischium, which extends beyond ilium; (c) protrusion subequal; (d) ischium protrudes beyond subequal pubis and ilium.
39. Fusion of pubes: (a) unfused; (b) fused.
40. Dorsoventral width of postacetabular ilium: (a) narrow; (b) moderately wide; (c) very wide.
41. Preacetabular tuberculum: (a) elongate; (b) short; (c) absent.
42. Dorsoventral width of pubis and ischial bar: (a) ischial bar markedly wider than pubis; (b) subequal.

Femur

43. Caudal margin of proximal antitrochanteric articular surface: (a) highly concave; (b) moderately concave; (c) straight or nearly so.
44. Proximal extension of trochanteric crest and acetabular articular surface: (a) trochanteric crest extends moderately beyond acetabular articular surface; (b) subequal; (c) trochanteric crest extends far beyond acetabular articular surface; (d) acetabular articular surface extends beyond trochanteric crest.
45. Relationship of longest axis of shaft to longest axes of medial and lateral condyles: (a) parallel or nearly so; (b) divergent by 15 degrees or greater.

46. Extension of medial and lateral condyles: (a) subequal distally; (b) lateral condyle extends slightly distally beyond medial condyle; (c) lateral condyle extends distally far beyond medial condyle.
47. Dorsal margin of lateral condyle: (a) straight or nearly so; (b) moderately concave dorsally; (c) highly concave dorsally.
48. Distal extension of lateral condyle and fibular trochlea: (a) subequal or nearly so; (b) fibular trochlea extends $\frac{3}{4}$ or less of the distal extension of the lateral condyle.
49. Muscle impression near popliteal fossa: (a) well-developed; (b) absent or reduced.
50. Distal margin of medial condyle: (a) semicircular; (b) triangular or elliptical; (c) flattened.

Tibiotarsus

51. Mediolateral compression of cranial and lateral cnemial crests: (a) slight or no compression; (b) moderate compression; (c) substantial compression.
52. Extent of cranial cnemial crest and remaining articular surface in proximal view: (a) cnemial crest equal in extent to remaining articular surface; (b) cnemial crest less extensive than remaining articular surface; (c) cnemial crest more extensive than remaining articular surface.
53. Proximal extension of cranial cnemial crest: (a) moderately beyond articular surface; (b) slightly beyond articular surface; (c) far beyond articular surface.
54. Lateral margin between lateral cnemial crest and lateral articular surface: (a) shallowly concave; (b) deeply concave.
55. Channeling at margins of intercondylar eminence: (a) present; (b) absent.
56. Intercondylar eminence: (a) present; (b) absent.
57. Supratendinal pons: (a) present; (b) absent.
58. Location of area of extensor canal: (a) medial of the midline of the shaft; (b) at the midline of the shaft.
59. Ridge extending laterally from extensor canal: (a) present; (b) absent.
60. Craniodistal margin of lateral condyle: (a) semicircular; (b) elliptical.
61. Most cranial extension of lateral condyle: (a) at or near proximodistal midpoint of condyle; (b) markedly proximal of midpoint.
62. Caudal extension of lateral condyle: (a) moderate; (b) short; (c) long.
63. Lateral epicondylar depression: (a) shallow; (b) deep.
64. Width and length of medial condyle: (a) moderate; (b) moderate in width, short in length; (c) very wide, very short.
65. Comparative size of medial and lateral condyles in distal view: (a) subequal or nearly so; (b) medial condyle larger than lateral condyle.

Tarsometatarsus

66. Hypotarsus: (a) rectangular; (b) triangular; (c) narrow ridge.
67. Number of hypotarsal sulci: (a) three; (b) two; (c) one.
68. Location of hypotarsus: (a) lateral of midline of shaft; (b) at or very near midline.
69. Medial margin of proximal end: (a) ridged; (b) unridged.
70. Extension of hypotarsus and intercotylar eminence: (a) intercotylar area extends further proximally; (b) subequal; (c) hypotarsus projects further proximally.
71. Depression between intercotylar area and hypotarsus: (a) present; (b) absent.
72. Depths of medial and lateral cotylae: (a) subequal; (b) medial deeper than lateral; (c) lateral deeper than medial.
73. Number of subhypotarsal ridges: (a) three or two; (b) one.
74. Plantar surface: (a) slightly grooved or ungrooved; (b) deeply grooved.

- 75. Number of trochlea: (a) three; (b) two.
- 76. Distal extension of trochleae IV and II: (a) IV extends beyond II; (b) subequal; (c) II extends beyond IV.
- 77. Depths of trochleae: (a) moderate; (b) deep.
- 78. Medial and lateral margins of trochlea III: (a) not parallel; (b) parallel.

Pes

- 79. Number of phalanges of digits II, III and IV: (a) three-four-five; (b) three-four-four; (c) zero-four-five.
- 80. Proximodistal lengths of proximal phalanges: (a) III longest, IV shortest or III and IV subequal; (b) III longest, II shortest; (c) II longest; (d) II and III subequal, IV shortest.
- 81. Proximal margins of phalanges: (a) v-shaped; (b) straight.
- 82. Surface of articular cotylae of basal phalanges: (a) deep, curved; (b) shallow, flattened.
- 83. Distal phalanges: (a) claw-shaped; (b) straightened.

Table 1.—Character states of each taxon. The letters “a,” “b,” “c,” and “d” refer to the character states described in the Appendix for each character. The letter “m” stands for “missing” and indicates either that the element showing a character has not been found (e.g., forelimb elements of the Dinornithidae), or that one of the structures used in defining the character is absent (e.g., intercotylar eminence of the tarsometatarsus in Aepyornis). The letter “u” stands for “unclear” and indicates that the state of a character is uncertain in Aepyornis because the skeletal element is poorly preserved. The letter “p” stands for “polymorphic” and indicates that the taxon exhibits several states of a given character.

	Character																													
Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	
Dinornithidae	a	a	b	a	d	b	a	a	m	a	m	b	b	c	a	b	a	m	m	m	m	d	m	m	m	m	m	m	m	m
<i>Apteryx</i>	b	a	a	a	d	b	a	a	c	a	a	b	b	c	a	b	a	b	c	a	d	m	d	b	b	b	a	b	b	c
<i>Casuarius</i>	a	c	c	b	c	a	a	a	a	c	b	a	b	a	a	a	c	a	c	a	b	c	a	a	a	b	p	a	b	b
<i>Dromaius</i>	a	c	c	b	c	a	a	b	a	d	b	a	b	a	a	a	a	c	a	b	c	a	a	a	a	b	b	b	b	c
<i>Rhea</i>	a	a	a	b	b	b	a	b	a	b	b	b	c	b	a	a	b	a	b	a	c	b	a	a	a	a	b	b	b	a
<i>Struthio</i>	a	c	c	c	c	a	b	b	a	b	b	b	c	b	a	a	b	a	a	c	b	a	a	a	a	a	a	a	b	a
<i>Aepyornis</i>	c	c	a	a	d	b	p	b	b	a	c	b	b	c	u	a	b	b	a	b	a	u	a	u	u	u	b	u	b	u
Dromornithidae	a	b	a	b	c	b	a	b	a	b	c	a	p	a	b	a	b	a	a	b	a	c	b	b	a	b	a	b	p	c
Character																														
31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58			
Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Dinornithidae	m	m	m	a	a	a	p	a	a	p	a	b	a	p	b	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a
<i>Apteryx</i>	b	b	b	b	b	a	a	a	b	a	a	c	b	a	b	a	b	b	a	a	a	b	a	a	b	b	a	b	a	a
<i>Casuarius</i>	b	b	b	b	b	a	b	c	a	c	b	a	b	b	b	b	b	b	b	b	a	c	c	b	b	b	b	b	a	a
<i>Dromaius</i>	b	b	b	b	b	a	b	c	a	c	b	a	b	b	b	b	c	b	b	c	c	c	b	a	a	b	b	a	a	a
<i>Rhea</i>	a	a	b	a	b	a	c	b	a	a	b	b	b	b	c	c	b	b	c	c	c	c	b	a	a	a	b	a	a	m
<i>Struthio</i>	a	a	b	a	b	a	c	b	b	a	a	b	b	d	b	c	c	a	b	c	c	c	b	a	a	a	a	b	a	a
<i>Aepyornis</i>	u	u	u	u	a	a	b	d	a	c	u	a	c	a	b	a	a	a	a	a	c	b	b	b	b	a	b	a	b	a
Dromornithidae	b	b	a	b	b	b	c	a	a	c	b	c	b	b	b	a	b	b	b	b	b	a	c	b	b	a	a	b	a	b
Character																														
59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83						
Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Dinornithidae	a	a	a	a	b	a	a	c	b	a	a	b	b	a	a	a	a	c	p	p	p	b	a	a	a	a	a	a	a	a
<i>Apteryx</i>	a	a	a	a	b	b	a	a	c	b	b	a	b	a	a	a	a	a	b	a	b	a	d	a	a	a	a	a	a	a
<i>Casuarius</i>	a	a	a	a	b	b	a	c	c	b	b	c	a	b	b	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a
<i>Dromaius</i>	a	a	a	a	b	b	a	c	c	b	b	c	a	b	b	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a
<i>Rhea</i>	a	b	b	c	b	c	a	c	c	a	b	b	a	b	b	a	a	a	a	b	a	c	a	a	a	a	a	a	a	a
<i>Struthio</i>	b	b	b	c	b	c	a	c	c	a	b	b	a	b	b	a	a	m	a	b	c	b	a	a	a	a	a	a	a	a
<i>Aepyornis</i>	b	b	a	b	b	c	b	c	b	b	m	b	c	b	a	a	b	a	b	a	a	a	a	a	a	a	a	a	a	a
Dromornithidae	b	a	a	b	a	a	b	b	b	a	c	a	b	b	a	a	a	a	b	a	b	c	b	b	b	b	a	b	b	b

Table 2.—*Character coding. The sample below indicates the method for subdividing a character with multiple derived states (in this instance character 21) into several characters. A separate character is constructed for each derived state. Note that the coded characters retain the pattern of the uncoded shared derived character states. The character states "m" (missing), "u" (unclear), and "p" (polymorphic) were coded as unknown and are indicated by a question mark.*

Taxon	Uncoded state	Subdivided coded characters		
		1	2	3
Hypothetical ancestor	a	0	0	0
Dinornithidae	m	?	?	?
<i>Apteryx</i>	d	0	0	1
<i>Casuarius</i>	b	1	0	0
<i>Dromaius</i>	b	1	0	0
<i>Rhea</i>	c	0	1	0
<i>Struthio</i>	c	0	1	0
<i>Aepyornis</i>	u	?	?	?
Dromornithidae	a	0	0	0

A NEW SPECIES OF *SIPHOCYPRAEA* (GASTROPODA, CYPRAEIDAE)
FROM THE NEOGENE OF SOUTHWEST FLORIDA

JUAN J. PARODIZ

Curator Emeritus, Section of Invertebrate Zoology

ABSTRACT

A new fossil cowry, *Siphocypraea trippeana*, is described from the Buckingham Formation (early Pliocene; Petuch, 1987) in southwest Florida. The genus *Siphocypraea* (Miocene–Recent) is divided into three species-groups. *Siphocypraea hughesi* Olsson and Petit, and *S. transitoria* Olsson and Petit, both originally described as subspecies of *S. carolinensis* (Conrad), are elevated to species level.

INTRODUCTION

Intensive collecting carried out by Ms. Jay J. Tripp, Research Associate of Invertebrate Zoology (Carnegie Museum of Natural History), in the Newburn Mine, APAC Florida Inc. (Ashland Oil Inc.), Sarasota, Florida, during 1986–1987, produced a lot containing 24 gastropod specimens of the genus *Siphocypraea* that correspond to a new species described here. These, and many specimens of other extinct species of *Siphocypraea* collected by J. J. Tripp, are from the Buckingham Formation (early Pliocene).

The genus *Siphocypraea* Heilprin, 1887, ranged from North Carolina to southern Florida during the Miocene–Pliocene, although Recent species are restricted to the northern coast of South America. Extant species formerly placed in the *Cypraea mus* complex are now included in *Siphocypraea* (Petuch, 1979). Thus, *Siphocypraea* currently contains a number of species, and may be divided into three species-groups based on morphological features. The differences between these groups, however, are slight, and subgeneric separation is questionably justified. These groups are best considered under the concept of superspecies without taxonomic status. The genus *Cypraeacteon* White, from the Cretaceous–Paleocene of Brazil, was treated as a synonym of *Siphocypraea* by Wenz (1938). It has a shell more like *Marginella* than *Siphocypraea*, without labial or columellar teeth, and for these reasons it should not be included in the *Siphocypraea* grouping.

With *Cypraea mus* Linnaeus from the north coast of South America as type, Woodring (1957) established the subgenus *Muracypraea* within *Cypraea*; Olsson and Petit (1964) included it as a subgenus of *Siphocypraea*, while Petuch (1979) synonymized it under *Siphocypraea*. Gardner (1948) named a “section” *Akleistostoma* for species of the *Siphocypraea carolinensis* group, and this is here placed in synonymy. As Petuch (1979) indicated, the bulla stages of *S. mus* and *S. henekeni* Sowerby are similar to adult specimens of *Siphocypraea* in having a crater-like umbonal feature, supporting a congeneric grouping. This feature, inferred to be primitive, suggests that early fossil *Siphocypraea* are similar to the ancestral stock of the entire lineage.

SPECIES GROUPS

Three species groups are recognized on the basis of the following characters:

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- I. Adult state with apex having a crater-like depression. Aperture narrow and very regular, posterior canal very deep and circular with a comma-shaped sulcus; smaller fossula.
S. problematica Heilprin, 1887 (type of *Siphocypraea*)
S. lindae (Petuch, 1986)
S. trippeana n. sp.
- II. Adult state with apex having a crater-like depression. Aperture wider, irregular, almost circular at the anterior portion where the columellar and labial sides are concave. Posterior canal more elongated; comma-shaped sulcus less curved; larger fossula.
S. carolinensis (Conrad, 1841)
S. carolinensis floridana Mansfield, 1931
S. transitoria Olsson and Petit, 1964, new status
S. hughesi Olsson and Petit, 1964, new status
S. pilsbryi (Ingram, 1939)
S. chilona (Dall, 1900)
- III. Adult stage with regular *Cypraea*-like apex; aperture variable.
Recent: *S. mus* (Linnaeus, 1758)
Recent and Pleistocene:
S. henekeni (Sowerby, 1850) [Not *henekeni* as cited by Weisboard (1962), a misidentification of *S. donmoorei* Petuch]
S. donmoorei Petuch, 1979

SYSTEMATICS

Siphocypraea trippeana Parodiz, new species

Fig. 1, 5, 9, 11

Description.—Shell elongate, width slightly less than half the length; semioval, narrowed anteriorly, wider than high. Dorsum very convex, smooth. Base flattened anteriorly. Margin without regular pitting, outer area of lip faintly marked by projections of teeth. Callus thick in rostral view, but angulated on portion that turns over dorsum at anterior end; regularly curved from middle to posterior end, showing some weak undulations. Line separates callus from dorsum. Anterior canal projecting to right in opposite direction of apical notch. Edge of anterior canal forms sharp terminal ridge oblique to first columellar tooth; between these features is wide depressed area that enhances sharpness of ridge, flattened at ends below ridge. Similar but smaller flat area on opposite (labial) side, which has no ridge. Small fossula only visible in oblique view, as is inconspicuous columellar sulcus described above. Crater or pit of sunken apex keyhole-shaped, continuing from posterior deep canal, narrow below and widely projected to right above (posterior view), with portion corresponding to extension of outer lip semilunar; viewed dorsally, notch much wider than in related species; posterior opening covered by curved end of lip with margination around keyhole edge which thickens toward columellar side. Width of aperture constant from anterior to posterior end. Eighteen teeth on columellar side; anteriormost tooth forms angle with terminal ridge between which is depressed area; teeth regularly spaced anteriorly, irregular and uneven toward posterior end. Twenty-two labial teeth, very regular and well separated at middle, but closer and sharper near anterior canal; fourth labial tooth is at level of first columellar tooth. Teeth near posterior notch smaller. Shell solid, heavier than specimens of comparable size in other species.



Fig. 1–4.—*Siphocypraea* species. 1. Dorsal view of *Siphocypraea trippeana* (Holotype, CM No. 42199. Length, 55.8 mm). 2. Dorsal view of *S. problematica* (CM No. 43575. South bank of Caloosahatchee River, La Belle, Florida; coll. K.K. Shaw (1966). Length, 60 mm). 3. Dorsal view of *S. carolinensis floridana* (CM; Florida. Length, 76 mm). 4. Ventral view of *S. carolinensis floridana* (Same specimen as Fig. 3).

Dimensions (in mm).—Holotype (specimen No. 9 in lot, Carnegie Museum No. 42199). Length (L), 55.8; diameter (D), 32.2; height (H), 26.8; width of aperture, 3; width of anterior canal at middle, 2.5; depth of apical notch, 9; apical notch at widest dorsal point, 8.5.

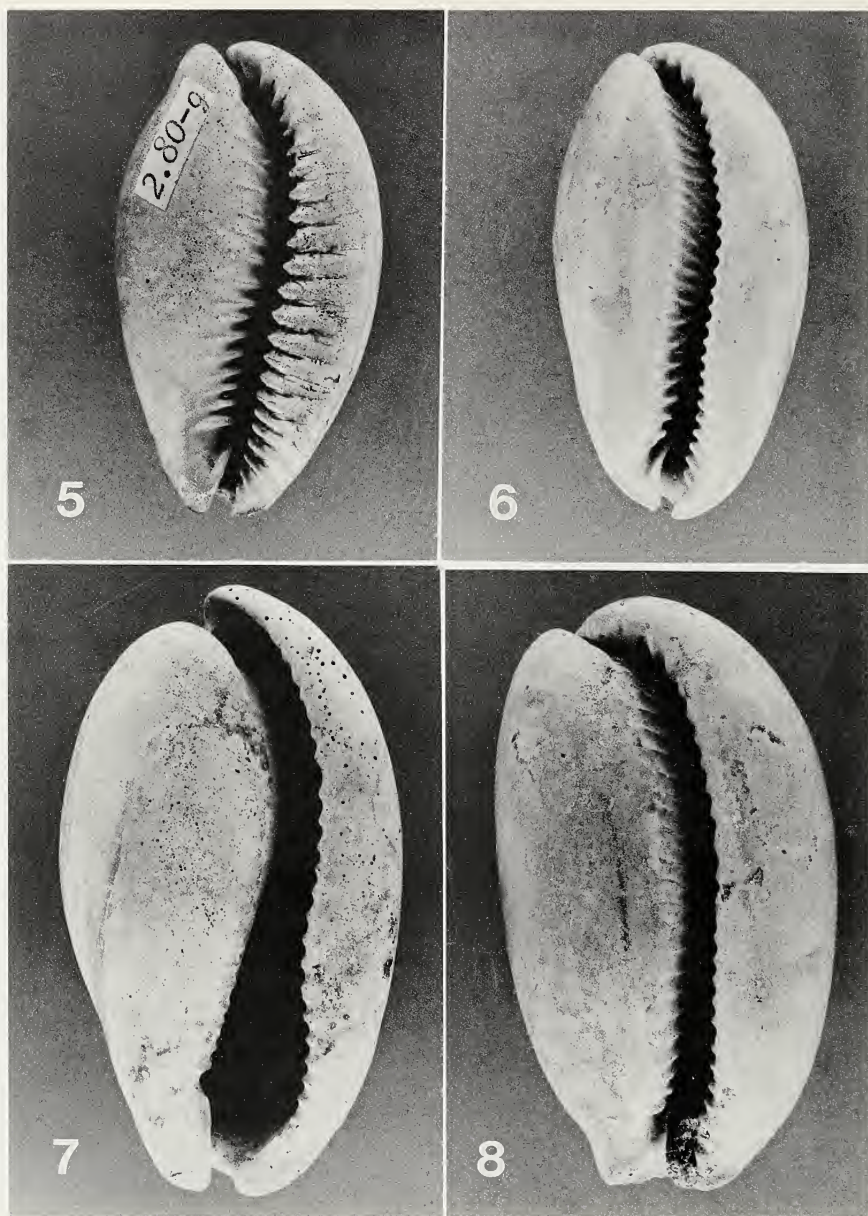


Fig. 5–8. — Ventral view of *Siphocypraea* species. 5. *Siphocypraea trippeana* (Holotype, CM No. 42199. Length, 55.8 mm). 6. *S. problematica* (CM No. 43575, same specimen as Fig. 2). 7. *S. carolinensis floridana* (CM No. 47179. Newburn Pit Mine, Sarasota, Florida; coll. J. J. Tripp (1983). Length, 89 mm). 8. Gerontic specimen of *S. problematica* (CM No. 43540. Banks of Lake Okeechobee, Florida; coll. E. Maratt (1960). Length, 78 mm).

Paratypes. 21 (18 perfectly preserved; 3 with fractured dorsum). The mean of all specimens measured is: L, 53.9; D, 30.7; H, 24.6; labial teeth, 20; columellar teeth 18–22. Ratios: L/D 1.73; L/H 2.19; D/H 1.24.

Variation. — In the type lot, specimens shorter than the type are narrower, the

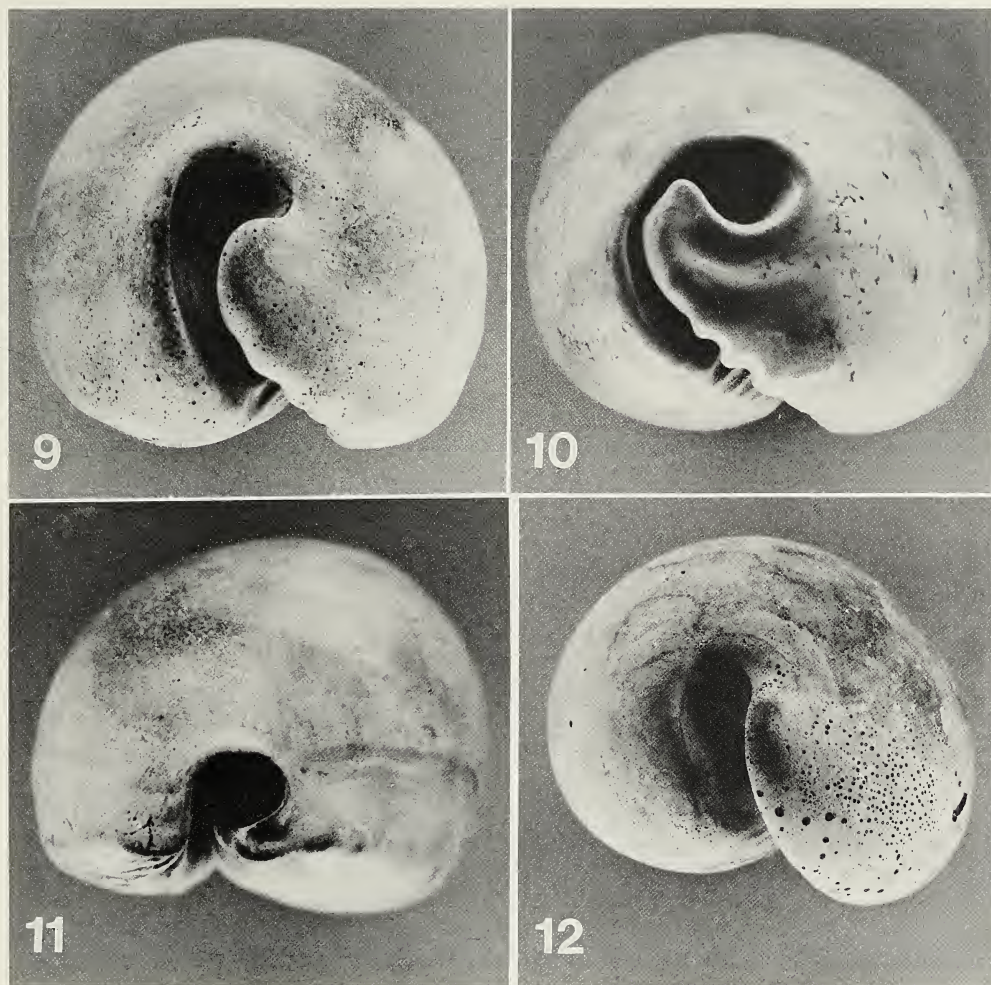


Fig. 9–12.—Anterior and posterior views of *Siphocypraea* species. 9. Posterior (apical) view of *Siphocypraea trippeana* (Holotype, CM No. 42199. Width, 32.2 mm). 10. Posterior view of *S. problematica* (CM No. 43575, same specimen as Fig. 2. Width, 34 mm). 11. Anterior view of *S. trippeana* (Holotype, CM No. 42199. Width, 32.2 mm). 12. Posterior view of *S. carolinensis floridana* (CM No. 47179, same specimen as Fig. 7. Width, 50 mm).

width increasing in larger specimens in greater proportion than the length. The number of labial and columellar teeth varies from 18 to 26, and 15 to 22, respectively, and in some cases the number of teeth increases proportional to the size of the shell, but there are also some large specimens with less teeth than average. The height increases according to the length of the shell but gerontic specimens are relatively higher.

Type locality.—Newburn Mine, APAC Florida Inc. (Ashland Oil Inc.), D.O.T. 17-087, in Buckingham Formation (Mansfield, 1939), early Pliocene (Petuch, 1987), Sarasota, Florida.

DIAGNOSTIC COMPARISONS

The species most similar to *S. trippeana* is *S. problematica*, the type of *Siphocypraea*. Both species are of comparable size, but normal adults of *S. problematica* are larger, particularly gerontic specimens (Fig. 8). In *S. problematica*, the anterior ridge is sharper and consequently the area between it and the first columellar tooth is more depressed. In *S. trippeana*, the apical opening is more of a keyhole shape (Fig. 9), not circular as in *S. problematica* (Fig. 10), and in dorsal view not as flat. Due to its shape, the opening extends over the dorsum more in *S. trippeana* where it is more visible than in *S. problematica* (Fig. 1, 2). Also, the comma-shaped sulcus characteristic of *S. problematica* is less rounded or curved in the new species, and the projecting lobe wider distally. The aperture in both species is of constant width, a character that distinguishes them from the *S. carolinensis* group (Fig. 4–8).

In *S. carolinensis* and *S. carolinensis floridana*, the aperture widens considerably at the anterior end, forming a circular opening and the sides of the aperture are relatively parallel only at the posterior end (Fig. 12). *Siphocypraea carolinensis* also has larger anterior and posterior canals. The shell is wider in *S. carolinensis* (Fig. 3) than in *S. trippeana*. Specimens of *S. carolinensis* and *S. carolinensis floridana* have larger shells than *S. trippeana* specimens of similar age, and their shells are thinner and lighter than the strong shells of *S. trippeana*. These differences can be found also between the new species and *S. transitoria*, in which the sulcus is narrower and curved.

From *S. hughesi* the differences are still more obvious: *S. hughesi* is the most rounded of all the species, with the aperture more curved at the ends, and larger in size but with a smaller lobular projection on the sulcus.

Siphocypraea carolinensis floridana, and other forms described originally as subspecies, *S. carolinensis hughesi* and *S. carolinensis transitoria*, are—as well as *S. trippeana*—from the Buckingham Formation. The type localities of *S. hughesi* and *S. transitoria* are the same (five miles east of Brighton, Highlands County, Florida). The latter two forms are sympatric and synchronic, and subspecific status is inappropriate since no more than one subspecies can inhabit the same area. Therefore, in view of their differences, they should be considered as separate species, *Siphocypraea hughesi* Olsson and Petit, and *Siphocypraea transitoria* Olsson and Petit.

I have observed the following additional specimens of *S. problematica* and *S. carolinensis*, which are gerontic and unusually large:

Siphocypraea problematica.—Banks of Lake Okeechobee. Coll. E. Maratt (1960), CM No. 43540 (Fig. 8). 78 × 46 mm and as high as wide. Shell very thick and heavy.

Siphocypraea carolinensis floridana.—Newburn Pit Mine, Sarasota, Florida. Coll. J. J. Tripp (1983), CM No. 47179 (Fig. 7, 12). 89 × 50 mm; aperture at anterior end is 20 mm wide. Labial teeth 23. Although it is a larger specimen than the *S. problematica* from Okeechobee, the shell is considerably thinner and lighter.

Other observed specimens of *S. problematica* are:

CM No. 43575. South bank of Caloosahatchee River, La Belle, Florida. Coll. K. K. Shaw (1966) (Fig. 2, 6, 10). Three specimens of medium size, beautifully preserved, still having the glaze on dorsum and on the ventral side. Labial teeth 27, columellar 23. Anterior ridge very sharp.

CM No. 46851. Caloosahatchee Formation, on route 80, west of La Belle, Florida. Coll. J. J. Tripp (1981).

CM No. 47200. Coll. J. J. Tripp (1987). Found together with *S. trippeana*; numerous specimens.

DISCUSSION

A recently described species, *Cypraea lindae* Petuch, 1986, from the Buckingham Formation at Miami, also belongs to the *S. problematica* group by virtue of its characteristic straight aperture (Fig. 6). It differs from *S. problematica* as well as from *S. trippeana* by the very strong and more separated labial teeth, and the very coarse dentition on the columellar lip. The posterior notch is smaller than in *S. trippeana*; the shell is also smaller in size but wider than *S. trippeana*, and has a higher hump.

Siphocypraea donmoorei Petuch, 1979, from Panama to the coasts of Colombia and Venezuela, appears as a living and intermediate lineage between the typical *Siphocypraea* of the Florida Miocene-Pliocene and those of the *S. mus* group.

ACKNOWLEDGMENTS

The new species is dedicated with great satisfaction and gratitude to its discoverer, Ms. Jay J. Tripp. I am also grateful to Dr. John E. Rawlins and Patricia A. Roble for photography and manuscript preparation.

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CHROMOSOMAL STUDIES OF BATS (MAMMALIA: CHIROPTERA)
FROM THAILANDCRAIG S. HOOD¹DUANE A. SCHLITTER
Curator, Section of MammalsJOAN I. GEORGUDAKI²SONGSAKDI YENBUTRA³ROBERT J. BAKER⁴
Research Associate, Section of Mammals

ABSTRACT

Chromosomal data are presented for 19 species that represent four families of bats collected during field studies in Thailand. The karyotypes of *Pteropus lylei*, *Megaerops niphanae*, *Emballonura monticola*, and *Megaderma spasma* are reported for the first time. The karyotype of *Pteropus lylei* ($2n = 40$, $FN = 72$) presents new diploid and fundamental numbers for the genus *Pteropus*. The chromosomal complement of *Megaerops niphanae* ($2n = 26$, $FN = 42$) is like that reported for Thailand populations of the closely related species, *M. ecaudatus*. Chromosomal data for *Emballonura monticola* ($2n = 24$, $FN = 44$) is the first reported for a species of the genus *Emballonura*. *Megaderma spasma* ($2n = 38$, $FN = 64$) and *M. lyra* ($2n = 54$, $FN = 104$) differ substantially in overall chromosomal morphology, and in G- and C-banding patterns. Karyotypes for the other chiropteran species examined were similar to those previously reported in the literature.

INTRODUCTION

The bat fauna of Thailand includes nine families, 33 genera, and approximately 93 species, ranking it as one of the world's most diverse chiropteran faunas (Lekagul and McNeely, 1977; Corbet and Hill, 1980). Despite this diversity, little is known concerning the systematics and distribution of the bats of Thailand (e.g., Thonglongya, 1974; Thonglongya and Hill, 1974; Hill, 1974; Hill and Thonglongya, 1972; Yenbutra and Felton, 1983). Undoubtedly, as scientific research continues in the country, new distributional records will be added and it is not unlikely that new forms may be discovered and described.

In the summer of 1983, the Carnegie Museum of Natural History, Hofstra University, Texas Tech University, Texas A&M University, and the Thailand Institute of Scientific and Technological Research supported field studies that resulted in a collection of 848 small mammals, including a large collection of bats.

¹ Department of Biological Sciences, Loyola University, New Orleans, LA 70118.

² Department of Biology, Faculty of Natural Science, University of Patras, Patras, Greece.

³ Thailand Institute of Scientific and Technological Research, 196 Phahonyothin, Bang Khen, Bangkok 9, Thailand.

⁴ Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409. Submitted 10 May 1987.

Table 1.—*Chromosomal data for bats examined in this study. Symbols are: 2n, diploid number; FN, fundamental number; SM, submetacentric; ST, subtelocentric; A, acrocentric.*

Taxon	Males	Females	2n	FN	X	Y	References
Family Pteropodidae							
<i>Rousettus amplexicaudatus</i>	2	1	36	68	SM	A	1, 2
<i>Pteropus lylei</i>	2	0	40	72	SM	A	1
<i>Cynopterus sphinx</i>	8	14	34	58	SM	A	1, 3, 4
<i>Megaerops niphanae</i>	3	5	26	42	SM	A	1
<i>Eonycteris spelaea</i>	4	4	36	66	SM	SM	1, 5, 6
<i>Macroglossus sobrinus</i>	2	4	34	60	M	A	1, 5
Family Emballonuridae							
<i>Emballonura monticola</i>	0	2	24	44	—	—	1
<i>Taphozous melanopogon</i>	4	6	42	64	SM	A	1, 7, 8
Family Megadermatidae							
<i>Megaderma lyra</i>	3	5	54	104	SM	A	1, 7
<i>Megaderma spasma</i>	2	1	38	64	ST	A	1
Family Rhinolophidae							
<i>Rhinolophus acuminatus</i>	7	7	62	60	ST	ST	1, 4
<i>Rhinolophus affinis</i>	2	0	62	60	ST	ST	1, 9
<i>Rhinolophus coelophyllus</i>	2	1	62	60	ST	ST	1, 4
<i>Rhinolophus luctus</i>	0	1	32	60	ST	A	1, 9
<i>Rhinolophus malayanus</i>	3	2	62	60	ST	ST	1, 4
<i>Hipposideros armiger</i>	6	3	32	60	SM	ST	1
<i>Hipposideros fulvus</i>	0	1	32	60	SM	A	1, 7, 10
<i>Hipposideros larvatus</i>	5	6	32	60	SM	ST	1, 4
<i>Hipposideros lekaguli</i>	3	1	32	60	SM	ST	1, 4

References are: ¹ This study; ² Haiduk (1983); ³ Ray-Chaudhari et al. (1968); ⁴ Harada et al. (1982); ⁵ Yong and Dhaliwal (1976); ⁶ Ando et al. (1980b); ⁷ Ray-Chaudhari et al. (1971); ⁸ Hood and Baker (1986); ⁹ Harada, Yenbutra, Yosida and Takada (1985); ¹⁰ Harada, Yenbutra, Tsuchiya and Takada (1985).

Material from this collection has formed the basis for evolutionary studies utilizing anatomical, histological, and ultrastructural methods (Hood, 1986; Phillips et al., 1987). Molecular, biochemical, and chromosomal banding studies of rodents and bats are in progress.

Chromosomal studies of bats from Thailand have reported standard (non-differentially stained) karyotypes for 25 species representing five families (Harada et al., 1982; Harada, Yenbutra, Yosida and Takada 1985; Harada, Yenbutra, Tsuchiya and Takada, 1985). In this paper, we present chromosomal data for 19 species representing four chiropteran families (Table 1). In cases where our data are similar to those in the literature, we give the information in Table 1 and the Specimens Examined. Species accounts are presented for those species where new observations or conclusions were obtained. Chromosomal data for vespertilionid bats are not reported here, but have been treated elsewhere (Bickham et al., 1986; McBee et al., 1986).

MATERIALS AND METHODS

All specimens examined were obtained from natural populations. Standard, G-, and C-band chromosomal preparations were obtained by in vivo bone marrow (Lee and Elder, 1980; Baker et al., 1982) and tissue culture methods (from ear and lung biopsies, Baker and Bass, 1979). G- and C-banding followed Seabright

(1971) and Stefos and Arrighi (1971) according to the protocol of Baker and Qumsiyeh (in press). A minimum of ten complete spreads was scored for each specimen in the analysis of G- and C-band preparations. All figures presented in this paper represent the complete chromosomal complements of single cells.

Microscopic slides and tissue culture cell lines are deposited in The Museum, Texas Tech University. Voucher specimens are deposited in the Section of Mammals, The Carnegie Museum of Natural History (CM), The Museum, Texas Tech University (TTU), and the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC).

SPECIMENS EXAMINED

Cynopterus sphinx.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88324, CM 87932, CM 87944, CM 87945, CM 88353, CM 88358, CM 88359, CM 88360, CM 88369, CM 88370, CM 99371); Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88424, CM 88425, CM 88427, CM 88428); Huai Kha Khang Wildlife Research Station, 15°32'N, 99°17'E (CM 87957); Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Pet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 87918, CM 87919, CM 87920, CM 87921, CM 87959).

Megaerops niphanae.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88444, CM 88448, CM 88449, CM 88452, CM 88672); Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88457).

Rousettus amplexicaudatus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Sap Fa Pha Wildlife Research Station, 15°32'N, 99°17'E (CM 88460); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88461); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87974).

Pteropus lylei.—Chonburi Prov.; Panatnikom Dist., Wat Loung (CM 87972, CM 87973).

Eonycteris spelaea.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 87983, CM 87984, CM 87985, CM 87986, TCWC 47470); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87978, CM 87980).

Macroglossus minimus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 879932, TTU 41247, TCWC 47471); Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 87990, CM 87991, CM 87992).

Emballonura monticola.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 87994, CM 87995).

Taphozous melanopogon.—Chumphon Prov.; Pathhiu Dist., 25 km E Ban Nimit Charoen, 10°54'N, 99°31'E (CM 88000, CM 88530, CM 88531, CM 88532, CM 88533, CM 88534, CM 88535, CM 88536, CM 88537).

Megaderma lyra.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88012); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88008, CM 88011, CM 88538, CM 88540, CM 88541, TTU 41249, TCWC 47474).

Megaderma spasma.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 88013, CM 88014, CM 88015).

Rhinolophus acuminatus.—Surat Thani Prov.; Muang Surat Thani Dist., Khao Tha Phet Nature Study Center, 5 km S, 2 km E Surat Thani, 09°06'N, 99°01'E (CM 88020, CM 88021, CM 88022, CM 88023, CM 88024, CM 88025, CM 88027, CM 88028, CM 88029, CM 88545, CM 88546); Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 88016, CM 88017, CM 88018).

Rhinolophus affinis.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88033, CM 88034).

Rhinolophus coelophyllus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, (CM 88039); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88037, CM 88038).

Rhinolophus luctus.—Surat Thani Prov.; Tha Chang Dist., 15 km N, 23 km W Ban Maruan, 09°18'N, 98°58'E (CM 88040).

Rhinolophus malayanus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88044, CM 88046, CM 88558, CM 88559).

Hipposideros armiger.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88066); Huai Kha Khang Wildlife Sanctuary, 3.7 km S, 1 km E Khao Nang Rum Wildlife Research Station, 15°27'N, 99°18'E (CM 88067, CM 88069); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°38'N, 99°18'E (CM 88053, CM 88055, CM 88060); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88064); Chumphon Prov.; Pathiu Dist., 9 km N, 25 km E Ban Nimit Charoen, 10°59'N, 99°32'E (CM 88052).

Hipposideros fulvus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°32'N, 99°18'E (CM 88081).

Hipposideros larvatus.—Uthai Thani Prov.; Lan Saka Dist., Huai Kha Khang Wildlife Sanctuary, Khao Nang Rum Wildlife Research Station, 15°29'N, 99°18'E (CM 88086, CM 88087, CM 88089, CM 88090, CM 88091, CM 88092, CM 88095); Huai Kha Khang Wildlife Sanctuary, 1.5 km W Khao Nang Rum Wildlife Research Station, 15°29'N, 99°17'E (CM 88097, CM 88106); Huai Kha Khang Wildlife Sanctuary, Tam Khe Nok, 3.6 km N, 2.6 km W Sanctuary H.Q., 15°32'N, 99°18'E (CM 88610, CM 88611).

Hipposideros lekaguli.—Chumphon Prov.; Pathiu Dist., 9 km N, 25 km E Ban Nimit Charoen, 10°59'N, 99°32'E (CM 88109, CM 88110, CM 88111, CM 88113).

SPECIES ACCOUNTS

Rousettus amplexicaudatus (Geoffroy)

2n = 36; FN = 68

The karyotype of this species was first reported by Haiduk (1983) for specimens from Papua New Guinea. The chromosomal complement of our specimens, assigned to the subspecies *R. a. amplexicaudatus* following Rookmaaker and Bergmans (1981), appears to be identical to those reported from Papua New Guinea. Chromosomal evolution within the genus *Rousettus* is extremely conservative; only two rearrangements distinguish *R. aegyptiacus*, *R. amplexicaudatus*, and *R. (Lissonycteris) angolensis* (Haiduk et al., 1981). The karyotype of *R. leschenaulti*, which is apparently sympatric with *R. amplexicaudatus* in Thailand, has an identical 2n = 36, FN = 68 non-differentially stained morphology (Ray-Chaudhari et al., 1968; Harada et al., 1982).

Pteropus lylei Andersen

2n = 40; FN = 72

The karyotype of *Pteropus lylei* is reported for the first time. The autosomes of this species include 15 pairs of metacentric-submetacentric, and three pairs of subtelocentric chromosomes (Fig. 1A). The X is a large submetacentric and the Y a minute acrocentric element. This karyotype is unique for the genus *Pteropus*. All previously reported karyotypes have had a 2n = 38, FN = 72 chromosomal complement (*P. giganteus*, Ray-Chaudhari et al., 1968; Datta, 1977; *P. macrotis*, *admiraltitatum*, *neohibernicus*, Haiduk, 1983). The difference between these karyotypes appears to be the presence of an additional pair of small banded chromosomes in *P. lylei*. The nature of the rearrangements that were involved in this variation was not apparent in our comparisons of standard, G-, and C-band preparations. *Pteropus lylei* is a small form of *Pteropus*, endemic to Southeast Asia and found commonly in lowland areas of Thailand. Andersen (1912) noted that *P. lylei* was distinguished from other taxa within the *Pteropus vampyrus* species group (including *P. giganteus*, *vampyrus*, *ariel*, and *intermedius*), and may represent an indigenous continental form of the *vampyrus* group. In a group that exhibits extreme chromosomal conservation, the chromosomal data presented here support the notion that *P. lylei* is a distinct form.

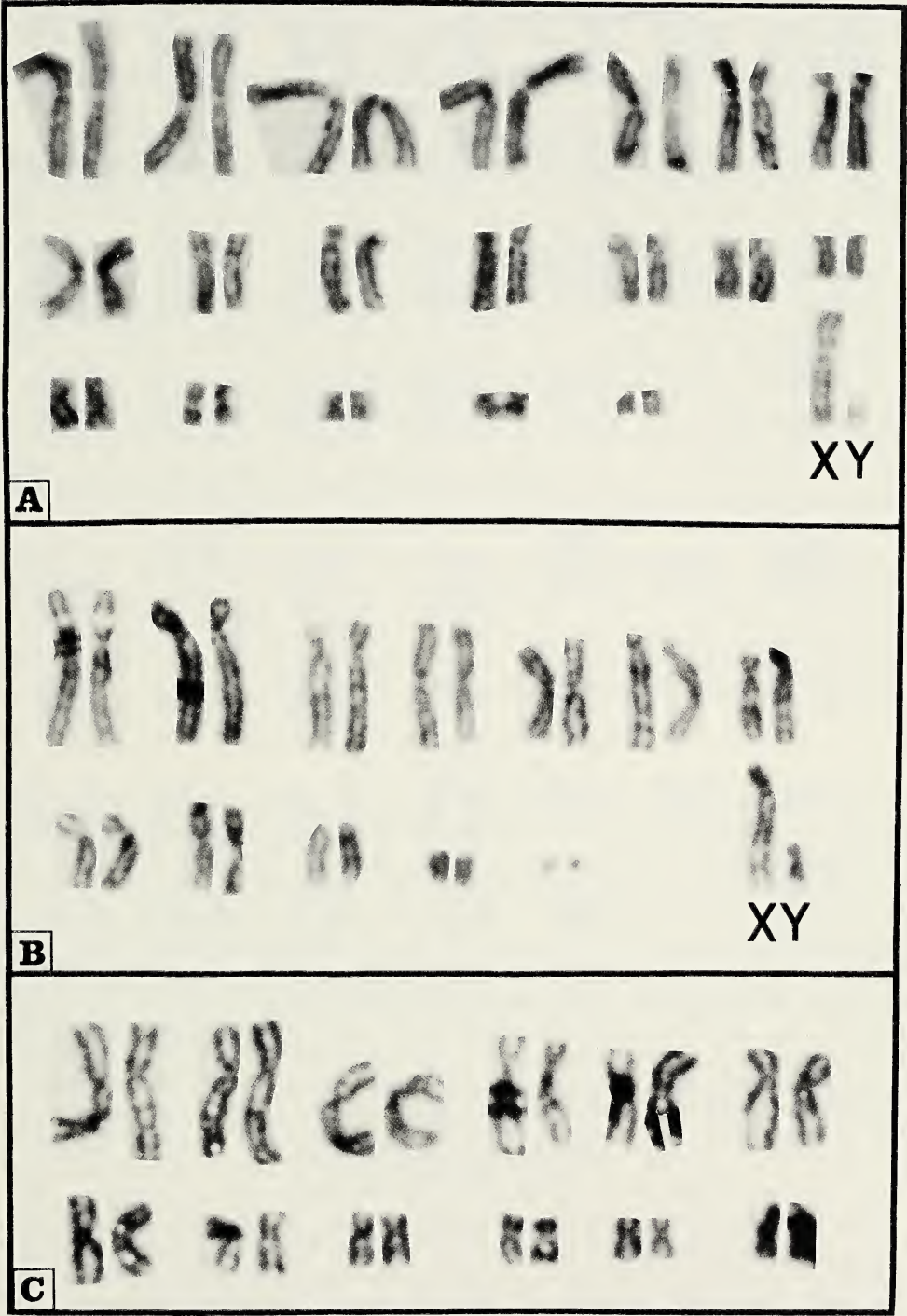


Fig. 1.—The standard karyotypes of: A) *Pteropus lylei*, male (CM 87973); B) *Megaerops niphanae*, male (CM 88672); C) *Emballonura monticola*, female (CM 87994).

Megaerops niphanae Yenbutra and Felton
 $2n = 26$; FN = 42

The karyotype of this recently described species is reported for the first time. The autosomes are comprised of nine pairs of metacentric-submetacentric, and three pairs of acrocentric chromosomes. The largest pair of autosomes has a prominent secondary constriction (Fig. 1B). The sex elements include a large submetacentric X and a small submetacentric or subtelocentric Y. This karyotype appears to be identical to that of some populations of the closely related species, *M. ecaudatus*. Populations of this species from central Thailand have a diploid number of 26, whereas bats from peninsular Malaysia are reported to have $2n = 24$ (Harada et al., 1982; Yong, 1984). Yong (1984) proposed that a Robertsonian translocation (fission/fusion event) involving the two largest acrocentric chromosomes of the $2n = 26$ karyotype accounts for the variation in diploid number. An alternative interpretation of the meaning of this chromosomal variation is that *M. ecaudatus* with the $2n = 26$ karyotype represents misidentified *M. niphanae*. In this case, the difference in diploid number represents differentiation between the two species. As currently understood, *M. ecaudatus* is restricted to peninsular Malaysia southward and *M. niphanae* is the proper specific epithet for *Megaerops* of central Thailand (Yenbutra and Felton, 1983).

Diploid and fundamental numbers are remarkably constant within the family Pteropodidae. Most pteropodids have diploid numbers of 34, 36, or 38 (Haiduk et al., 1980; 1981). However, the cynopterine taxa *Balionycteris* and *Megaerops* have radically departed from this trend with diploid numbers of 24 to 28 (Yong and Dhaliwal, 1976; Harada et al., 1982; Yong, 1984). Chromosomal banding data may provide a critical test of homology for these taxa.

Emballonura monticola Temminck
 $2n = 24$; FN = 44

Chromosomal data for *Emballonura monticola* is reported for the first time. Based on our examination of two female specimens, the karyotype is comprised of entirely biarmed chromosomes (Fig. 1C). Specific identification of the X and Y must await chromosomal data from a male. This is the first description of a karyotype of a bat of the genus *Emballonura*. Diploid numbers for the family Emballonuridae range from 22 to 32 for Neotropical taxa (Hood and Baker, 1986); four species of *Taphozous* examined to date all have $2n = 42$ (Ray-Chaudhari et al., 1971; Harada et al., 1982; Hood and Baker, 1986). C-band preparations showed that heterochromatin is restricted to centromeric regions, a pattern that has been found in most other emballonurids (Hood and Baker, 1986). Comparison of G-band patterns of *E. monticola* and other emballonurid genera failed to document any obvious banding homologies.

Megaderma lyra Geoffroy
 $2n = 54$; FN = 104

The karyotype of our specimens of *Megaderma lyra* (Fig. 2) appears to be identical to that reported for specimens from India (Ray-Chaudhari et al., 1971). C-band preparations show that C-positive material occurs extensively among the autosomes of this species. Heterochromatin was found in the long arms of six pairs (Fig. 2B). The incorporation of this magnitude of C-positive material is striking when compared with patterns of heterochromatin found in *M. spasma* (see below) and in other bat families. Heterochromatic material is primarily re-

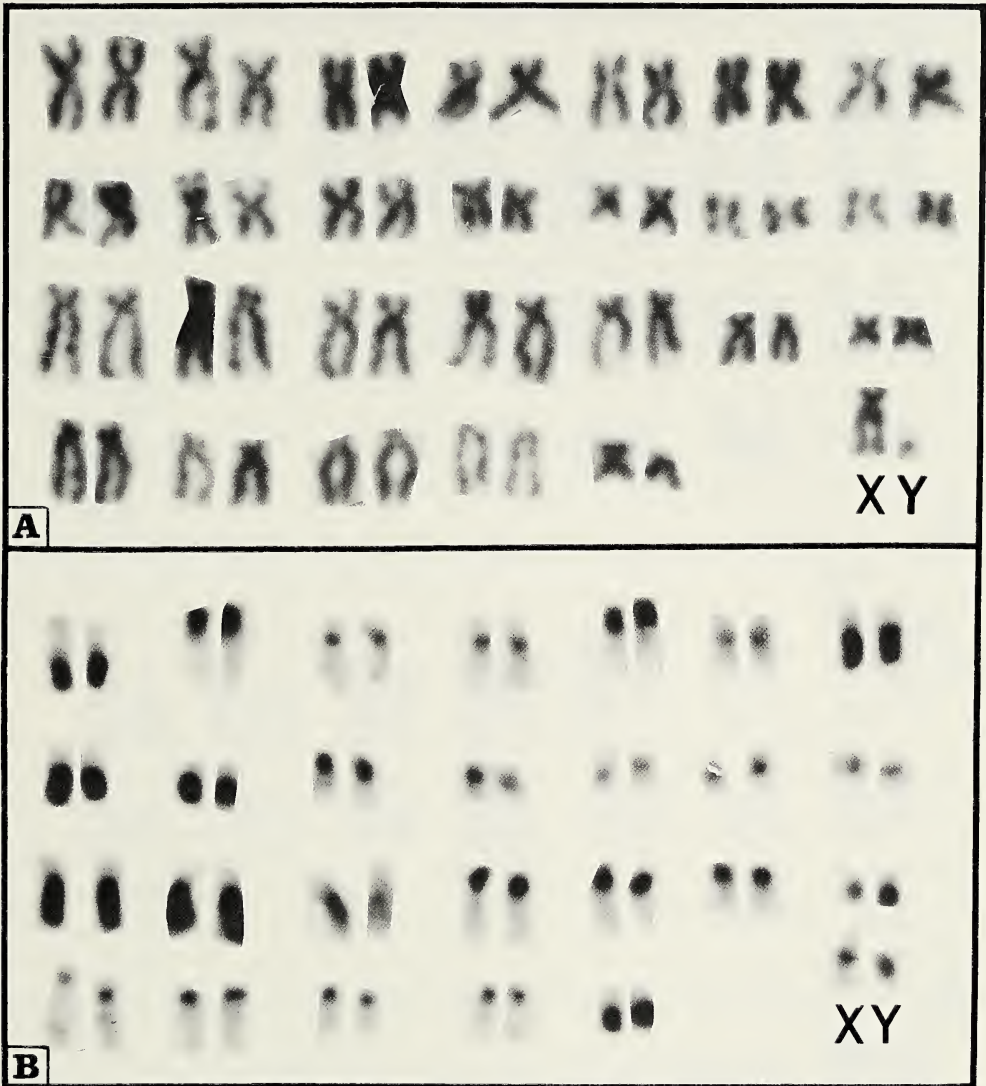


Fig. 2.—The standard and C-banded karyotypes of *Megaderma lyra*: A) male specimen (CM 88011); B) male specimen (CM 88012).

stricted to centromeric regions in Pteropodidae, Emballonuridae, Rhinopomatidae, Rhinolophidae, Phyllostomidae, Vespertilionidae, and Molossidae (Baker, 1979; Baker et al., 1982, 1987). Significant variation in the amount and placement of heterochromatin has been found in *Scotonycteris* (Pteropodidae, Haiduk et al., 1981), *Cormura* (Hood and Baker, 1986), and within the phyllostomids *Carollia*, *Choeroniscus*, *Tonatia*, and *Uroderma* (Baker, 1979; Baker et al., 1982).

Comparison of the G-band karyotypes of *Megaderma lyra* and *M. spasma* showed that extensive G-band repatterning has occurred during the evolution of these species. The lack of G-band resolution may be due to the heterochromatization of the autosomes in *M. lyra*, but may also reflect the fact that one or both

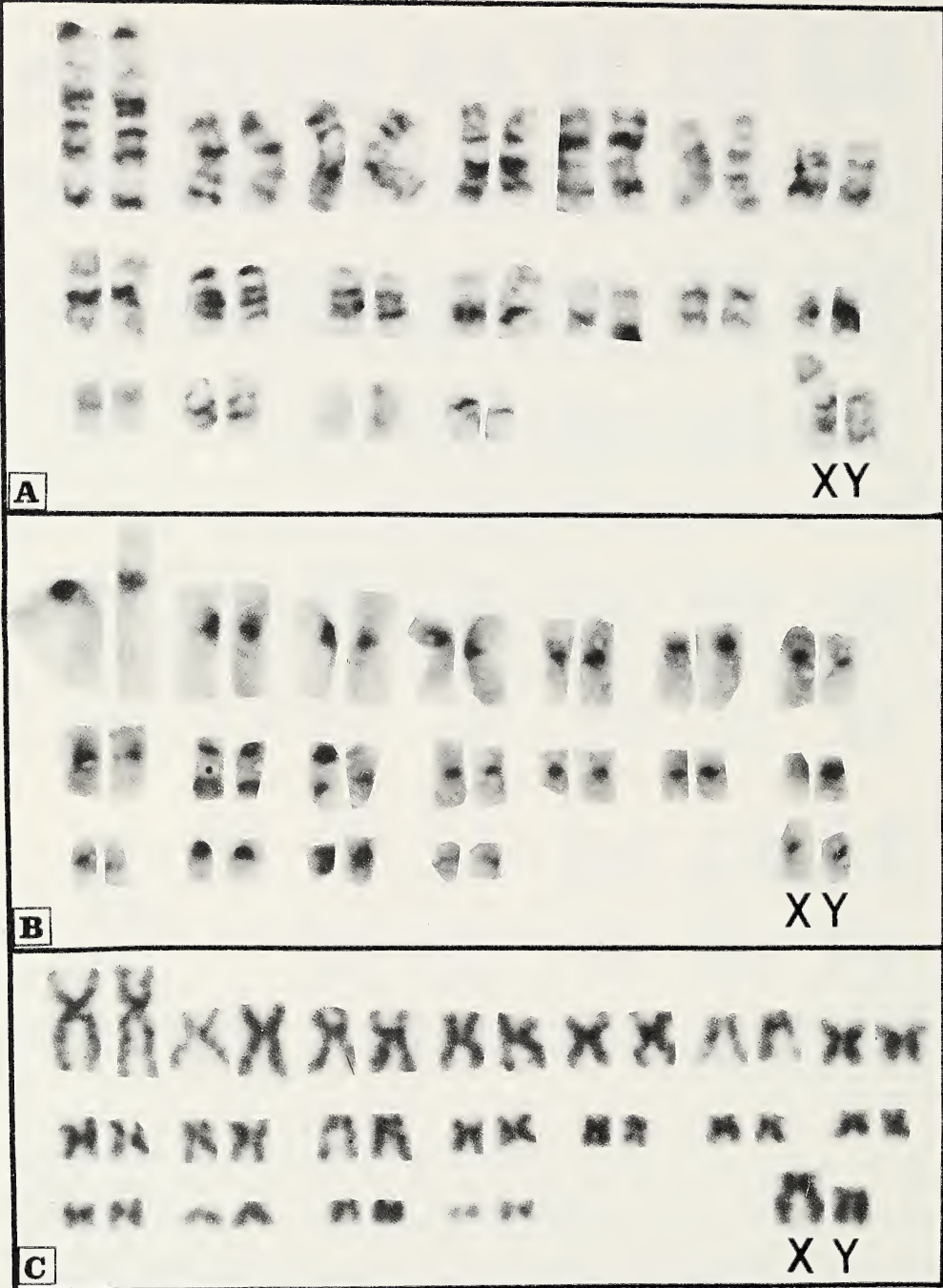


Fig. 3.— The karyotype of *Megaderma spasma*, male (CM 88015): A) G-banded karyotype; B) C-banded karyotype; C) standard karyotype.

taxa have undergone extensive euchromatic evolution since the establishment of ancestral generic conditions.

Megaderma spasma (Linnaeus)

$2n = 38$; $FN = 64$

The karyotype of *Megaderma spasma* is reported for the first time. The autosomes of this species include 14 pairs of metacentric-submetacentric, and four pairs of acrocentric chromosomes (Fig. 3). The largest autosome is nearly two times the length of any of the other chromosomes in the karyotype. The sex chromosomes include a medium-sized subtelocentric X and an acrocentric Y.

Heterochromatin is restricted to centromeric regions in most autosomes; telocentric C-positive material is found in two autosomes (Fig. 3B). G- and C-band karyotypes were compared with those of *M. lyra*, as well as with representatives of the families Pteropodidae, Emballonuridae, and Rhinopomatidae (Haiduk et al., 1981; Qumsiyeh and Baker, 1985; Hood and Baker, 1986). As noted above in the account on *M. lyra*, G-band homologies could not be demonstrated between the karyotypes of the two species of *Megaderma*. Furthermore, comparisons with other chiropteran families failed to document any obvious G-band homologies. A better understanding of the type, magnitude, and direction of chromosomal evolution within the Megadermatidae must await critical examination of chromosomal banding data for other species within the family.

Rhinolophus luctus Temminck

$2n = 32$; $FN = 60$

Two very different karyotypes have been reported for this species. Ando et al. (1980a) reported a diploid number of 52 for *Rhinolophus luctus* from Taiwan, whereas specimens from India and Thailand have been recorded as $2n = 32$ (Naidu and Gururaj, 1984; Harada, Yenbutra, Yosida and Takada, 1985). The karyotype of our female specimen from Ban Maruan is identical to that reported by Harada, Yenbutra, Yosida and Takada (1985) for specimens from Chiang Mai in northern Thailand. Harada, Yenbutra, Yosida and Takada (1985) suggested that the similarity in the karyotypes of *R. luctus* and species of *Hipposideros* ($2n = 36$) reflects chromosomal homology that may represent the ancestral karyotype for rhinolophids and hipposiderids. Given the large number of examples documenting that non-differentially stained karyotypes may be poor indicators of homology in bats (Haiduk et al., 1981; Baker et al., 1985, 1987; McBee et al., 1986) this conclusion seems premature. However, the differences between sub-specifically differentiated populations of *R. luctus* are striking. Intraspecific variation in bats usually involves one or a few rearrangements (Baker, 1979). Most examples of chromosomal polymorphism in bats have been associated with the hybridization of chromosomal races (Baker, 1979, 1984), or involve cases of cryptic species (Baker, 1984; Baker et al., 1985). The significance of chromosomal variation within *R. luctus* is not clear at this time.

Hipposideros armiger (Hodgson)

$2n = 32$; $FN = 60$

The karyotype of this species was first reported by Ando et al. (1980a) for specimens from Taiwan. The chromosomal complement of our specimens from Thailand, assigned to the subspecies *H. a. armiger*, appears to be identical to that reported from Taiwan. As in all species of *Hipposideros* examined to date,

the autosomal complement of *H. armiger* consists of a graded series of biarmed chromosomes. The X is a large subtelocentric and the Y is a medium-sized acrocentric element.

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TYPES OF MOLLUSCA IN THE COLLECTION OF THE
CARNEGIE MUSEUM OF NATURAL HISTORY.
PART I. BIVALVIA AND GASTROPODA
(PROSOBRANCHIA AND OPISTHOBANCHIA)

JUAN J. PARODIZ

Curator Emeritus, Section of Invertebrate Zoology

JAY J. TRIPP

Research Associate, Section of Invertebrate Zoology

INTRODUCTION

A very important part of the collection in the Section of Invertebrate Zoology at the Carnegie Museum of Natural History is that of the "types" of Mollusca. The present list includes lots of such materials in which the following categories of primary types, and information on each taxon, are indicated:

Holotype.—The original specimen selected by the author at the time of description of the taxon. If the lot corresponds, in our collection, to a category other than that of holotype, then the location of that holotype in another museum's collection is indicated.

Paratype(s).—According to Recommendation 73D of the International Code of Zoological Nomenclature (1985), "After the holotype has been labelled, each remaining specimen (if any) of the type-series should be labelled 'paratype,' in order to identify the components of the original type-series." Under such a definition, paratype material (all the specimens included by the author at the time of description) are not necessarily from the type locality. A distinction (not clearly indicated in the Code) should be made between "type-lot" and "type-series." The type-lot is that lot containing the primary type specimen (and paratypes if any) and is, of course, from the type locality. The type-lot, together with the other lots observed by the author, form the type-series.

Syntypes.—When the original lot contains more than one specimen without a holotype (or simply "type") having been selected, the specimens are called syntypes. This is the case with many old lots formerly called "co-types" (International Code of Zoological Nomenclature, Article 73B).

Lectotypes.—When, in a type series a holotype has not been designated, any author may designate one of the specimens as the lectotype by the use of that term or other appropriate expression. It may be that the lectotype was selected subsequent to the original description by the same or a different author, and if so, the information pertaining to lectotypes in this collection is indicated herein, provided that such lectotype has been legalized in publication, not simply on labels. When a lectotype has been properly designated, all other specimens in the type-series become *paralectotypes*. One additional lectotype is designated herein.

Neotypes.—A specimen may be selected by an author as a neotype when the primary type and paratypes are lost. It must agree as closely as possible with the

original description and should be obtained from or near the type locality, if possible. Other specimens, if any, in the same lot become *paraneotypes*. One additional neotype is designated herein.

"Topotypes."—These are specimen(s) collected at the type locality, and are not actually types, strictly speaking, having no validity in zoological nomenclature. Obviously, mention of such material is unnecessary, except in a revision of the species. Some "topotypes" in the Carnegie collection assume considerable importance because they belong to very rare species and are cited herein.

Family names.—The indication of the family to which each taxon belongs is that of the most current classification.

Nomenclature, numbers, etc.—Each type lot is here listed with the name under which it was originally described, with reference to the journal where it appeared. Names proposed as varieties (infrasubspecific) are indicated by the abbreviation "var." Following the original citation is the name change, if any, new combination, or valid senior synonym according to current nomenclature. Status is given for type materials in the Carnegie collection, and for those in other collections where the primary type or other paratypes are located.

The type localities listed in this catalog are for specimens in the Carnegie Museum. In a few instances, these are localities for secondary types (paratypes, paraneotypes, paralectotypes) which differ from the locality of the primary type (lectotype, neotype, or holotype).

A list of "type" materials in our collection was published by the Museum in 1931 by Dr. S. T. Brooks. The additions during the past 56 years doubled the number of species listed. The previous list did not give complete references and most of the materials were indicated as "part of type lot," "co-types," etc. Specimens in Brooks' list that are not bonafide types are not included in this catalog.

Many specimens that were part of the original type-series in the Academy of Natural Sciences in Philadelphia (ANSP), were received by our Museum from Dr. H. A. Pilsbry in the early years of this century. These specimens came with revised labels corrected *after* the time of original publication. When the condition of such "type" specimens was verified, the name listed herein is the original, not the one that appears on the labels. The corrected name is, of course, also indicated. In other cases, the original Pilsbry description gave no indication of types, so the materials received from him, or from Dr. S. Hirase of Kyoto (who provided Dr. Pilsbry with parts of the many type-series of Japanese shells), had to be registered as syntypes (or paratypes, when further information was available). During 1930–1948, when Pilsbry produced his large monographs of the "Land Shells of North America," he included in his revision of many of the species a "type" with illustrations, and with catalog numbers at the ANSP, which was not indicated in the original description. All these are *subsequent selections* and as such are not a subject for discrimination in our catalog. To simplify matters, such "type" indications by Pilsbry are here accepted, and Carnegie lots for such type-series are marked as paratypes.

Original citations could not be found for names referring to a small number of specimens marked as types in the collection. These names are included in this catalogue, but are clearly marked as problematic. These names include some attributed to O. F. Möllendorf, C. Torre, and P. Bartsch (as listed by Fluck, *The Nautilus*, 20(1):4, 1906). Some of these names are undoubtedly *nomina nuda*.

It may seem unnecessary to emphasize the importance of the type concept in taxonomic procedure. However, it is noteworthy to remember that no type-spec-

imen is necessarily "typical" or average; such a condition can only be established statistically when a sufficient number of specimens from several localities in the species' range are considered. Even when the type material consists of a unique specimen, its real value is for identification of the species bearing the name the type specimen represents. Any "standard" specimen is more theoretical than real, as a single specimen can not represent all variations of the *hypodigm* (the totality of specimens known). In spite of the fact that most research is now conducted at the level of populations, the accurate recognition of types will continue to be a requirement for a useful and unambiguous nomenclature.

ORGANIZATION OF THE CATALOG

The major divisions in this catalog correspond only to classes and subclasses of Mollusca as follows:

Part I. Class Bivalvia

Subclass Filibranchia

Subclass Eulamellibranchia

Class Gastropoda

Subclass Prosobranchia

Subclass Opisthobranchia

Part II. Class Gastropoda

Subclass Pulmonata

Names for taxa of the species-group are listed alphabetically within the corresponding subclass. Family names indicated after each trivial name are those of general acceptance as in Wenz-Zilch, 1938–1960 for Gastropoda (Handbuch der Palaeozoologie). In some cases, where the correct family placement of a genus is uncertain, as in the "Hydrobiidae," the family name is used *sensu lato*.

Some species or subspecies of *Pisidium* (Sphaeriidae) described by Sterki in 1922 (Annals of Carnegie Museum, 13:425–439) about which the author said that the "types" or "type lots" were in the collection of the Carnegie Museum, have not been found. These are: *P. compressum mutatum*, *P. decisum*, *P. apiculatus*, *P. notophthalmi*, *P. orcasense*. It must be noted that when Dr. Brooks catalogued the types of Bivalvia in 1931, he did not include *Pisidium*. Afterwards we were able to locate 11 "type lots" in the collection, all syntypes and synonyms of other species (See: Kuiper, Monograph of Australian Sphaeriidae, Basteria, (1983):47: 3–52, comments on Sterki, p. 8). For a complete synonymy of the genus *Diplodon*, see Parodiz, 1968, Sterkiana, 30.

For brevity, initials are omitted from all author names used in this catalog with the exception of A. Adams, C. B. Adams, H. Adams, F. C. Baker, and H. B. Baker. An alphabetical list of all other author names with initials follows: C. G. Aguayo, T. H. Aldrich, J. A. Allen, J. G. Anthony, S. Archer, B. W. Arnold, H. G. Askew, B. R. Bales, P. Bartsch, J. Benkert, J. Bequeart, P. Bermudez, S. S. Berry, P. Biolley, W. Blume, A. A. Bonetto, S. T. Brooks, J. A. Burke, R. E. Call,

A. Carcelles, E. P. Cheatum, W. F. Clapp, H. W. Clark, W. J. Clench, P. A. Conrad, C. M. Cooke, Jr., L. E. Daniels, P. G. Deschayes, W. D. Doherty, R. J. Drake, E. Duarte, R. W. Dunker, C. C. Engberg, W. J. Eyerdam, W. H. Fluck, L. S. Frierson, S. L. H. Fuller, L. Germain, D. Geyer, G. F. Gmelin, H. H. Godwin-Austen, C. Goodrich, A. A. Gould, A. F. Gray, F. Haas, S. S. Haldeman, A. W. Hanham, W. D. Hartman, J. D. Haseman, J. B. Henderson, Jr., R. Herbst, H. B. Herrington, A. A. Hinkley, S. Hirase, C. C. Hoff, F. R. Holland, L. Hubricht, H. von Ihering, R. Jackson, M. L. Jaume, R. I. Johnson, T. Kira, R. J. Kirkland, M. Klappenbach, J. G. J. Kuiper, F. R. Latchford, I. Lea, J. Lewis, G. MacMillan, M. C. D. Mansur, E. von Martens, W. G. Maton, R. A. McLean, N. de Medina, J. R. Miller, H. Modell, O. F. Möllendorf, T. di M. A. Monterosato, A. Morelet, J. P. Morrison, G. Nelson, W. Newcomb, O. O. Nylander, W. Old, A. d'Orbigny, A. Ortmann, K. Palmer, J. J. Parodiz, W. H. Pease, E. Pfeiffer, H. A. Pilsbry, F. Poey, G. S. Poli, C. Porter, T. Prime, S. Putzey, C. S. Rafinesque, L. A. Reeve, H. Rehder, S. N. Rhoads, H. G. Richards, T. Say, H. van der Schalie, G. Schwab, C. T. Simpson, H. H. Smith, V. Sterki, W. S. Strode, J. Thiele, J. N. Thomas, F. G. Thompson, C. Torre, J. J. Tripp, W. I. Utterback, M. J. Viana, J. A. Wagner, B. Walker, H. E. Wheeler, R. Wichmann, C. B. Wilson, and B. H. Wright.

Question marks placed after names of taxa indicate uncertainty in placement of genera within families, or species within genera. The expression "coll." before or after a name indicates, but does not distinguish between, the original collection in which the specimens resided and the actual collector of the specimens.

NEW COMBINATIONS

The following new combinations are proposed in alphabetical order of species names:

- Licina megacheilos apreitensis* (Baker) NEW COMBINATION, formerly *Tudora megacheilos apreitensis* Baker, 1924.
Licina fossor arubana (Baker) NEW COMBINATION, formerly *Tudora fossor arubana* Baker, 1924.
Lyrodes cheatumi (Pilsbry) NEW COMBINATION, formerly *Potamopyrgus cheatumi* Pilsbry, 1935.
Chondrothyrella (Plicathyrella) claudicans (Poey) NEW COMBINATION, formerly *Cyclostoma claudicans* Poey, 1858.
Hendersonina (Hendersonina) hendersoni (Torre) NEW COMBINATION, formerly *Chondropoma hendersoni* Torre, 1909.
Licina nelsoni (Clapp) NEW COMBINATION, formerly *Colobostylus nelsoni* Clapp, 1914.
Annularia andrerosae roatanensis (Richards) NEW COMBINATION, formerly *Choanopoma andrerosae roatanensis* Richards, 1938.
Licina aurantia wassauensis (Baker) NEW COMBINATION, formerly *Tudora aurantia wassauensis* Baker.
Licina fossor westpuntensis (Baker) NEW COMBINATION, formerly *Tudora fossor westpuntensis* Baker, 1924.

ACRONYMS

The following abbreviations are used in Part I for major institutional collections:

- ALA Alabama Museum of Natural History, University of Alabama, Tuscaloosa, Alabama

ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania
BMNH	British Museum (Natural History), London, England
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
FMNH	Field Museum of Natural History, Chicago, Illinois
ISU	Indiana State University, Terre Haute, Indiana
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina
MCZ	Museum of Comparative Zoology, Harvard University, Boston, Massachusetts
MNHN	Museo Nacional de Historia Natural, Montevideo, Uruguay
MZUM	Museum of Zoology, University of Michigan, Ann Arbor, Michigan
OSM	Ohio State Museum, Columbus, Ohio
SMF	Senckenberg Museum, Frankfurt am Main, Germany
UCM	University of Colorado Museum, Boulder, Colorado
UF	University of Florida, Gainesville, Florida
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

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CATALOG OF TYPES

Bivalvia

Subclass Filibranchia

- balesi* Pilsbry and McLean, 1939. *Arca* (*Barbatia*) ARCIDAE
 Notulae Naturae, 39:1, text fig. 1
 = *Barbatia tenera* (C. B. Adams, 1845)
 CM, 1 Paratype (type-series), 42751 (ex-Bales)
 Type Locality: Missouri Key, Florida
- circumpicta* Pilsbry, 1904. *Ostrea* OSTREIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 56:
 559, pl. 40, figs. 12–13
 CM, 1 Paratype (type-series), 61.9034 (ex-Hirase 500)
 Type Locality: Hirado, Hizen, Kyushu, Japan
- hirasei* Pilsbry, 1901. *Lima* LIMIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:
 209, pl. 19, fig. 9 (figure indicated as *hians* var. *hirasei*)
 CM, 6 Syntypes, 61.9044 (ex-Hirase 901); labelled by Hirase as *Lima*
hians hirasei Pilsbry
 ANSP, Syntypes, 80525
 Type Locality: Hirado, Hizen, Kyushu, Japan
- japonicum* Pilsbry, 1905. *Trapezium* TRAPEZIIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 57:
 119, pl. 5, figs. 34–36

CM, 6 Paratypes (type series), 61.9049 (ex-Hirase 1622)

Type Locality: Tsudla, Awa (Tokushima Prefecture), Shikoku, Japan

Subclass Eulamellibranchia

aetheopiformis "Ihering" (in *litteris*) Simpson, 1914. *Unio* HYRIIDAE

A Descriptive Catalogue of the Naiades or Pearly Fresh-water Mussels. Part 3. Bryant Walker, Detroit. P. 1312 (*Nomen nudum*)

= *Diplodon parallelipipidon aethiops* (Lea), see Parodiz, 1968, *Sterkiana*, 30:11, note 1.

CM, 1 whole and 3 single valves, Syntypes, 61-92 (ex-MZUM from Ihering's original lot)

MCZ, 2 Syntypes, 19236 (ex-Putzey coll.)

Type Locality: Rio Camaquam, Rio Grande do Sul, Brazil

alleni Sterki, 1912. *Pisidium* SPHAERIIDAE

The Nautilus, 26(1):9

= *Pisidium casertanum* (Poli)

CM, 4 Syntypes (of type series), 5871 (ex-Allen), Hebron, Oxford Co., Maine

Type Locality: Westbrook, Maine

analoga Ortmann, 1918. *Fusconaia cor* var. UNIONIDAE

Proceedings of the American Philosophical Society, 57:533

= *Fusconaia edgariana* (Lea)

The variety *analoga* was described as corresponding to *Fusconaia cor* [*Unio*], but two labels in Ortmann's materials indicate: *Fusconaia edgariana* var. *appressa*, and *F. edgariana analoga* (Ortmann). Compared with the description, and the type of *Unio cor* Conrad in the MCZ, *analoga* has no close relation with that species. Other lots of *analoga*, collected and labelled by Ortmann, from Virginia, Tennessee and Alabama, offer no differences with *edgariana*. Ortmann inferred that the specimen (in the British Museum) figured by Reeve in *Conchologia Iconica*, 16:65, "*Unio edgarianus* Lea," is his *analoga*; on account of that, Johnson (1977, *Occasional Papers, Mollusca, Museum of Comparative Zoology*, 4(58):236) selected that figured specimen as "holotype." Ortmann actually did not see this specimen, and his description was based on the syntypes he collected, with the type location of Speers Ferry, Clinch River, Scott Co., Virginia, 1913, CM 61.6526, 4 males and 4 females. Reeve's figured specimen is from Tennessee, which does not correspond to the type locality. Thus a lectotype is selected here from Ortmann's syntypes (specimen #1 of "type-lot"). It is a synonym of *edgariana*. For other observations and comparisons, see Parodiz 1967, *Sterkiana*, 28:23.

bernardi Pilsbry, 1904. *Spisula (Oxyperas)* MACTRIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:

550, pl. 39, figs. 4-6

= *Oxyperas bernardi* (according to Kira, 1962)

CM, 3 Syntypes, 61.9082 (ex-Hirase 1561, and ANSP)
Type Locality: Fukura, Awaji, Honshu, Japan

berthae Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 8:528, pl. 28, figs. 2–4; pl. 46, fig. 6
= clinal form of *Diplodon piceus* (Lea)
CM, Lectotype (Specimen #24, subsequent designation by Parodiz, 1968), 61.5865.
CM, 11 Paralectotypes, 61.5865 (ex-Haseman)
MCZ, Paralectotypes, 100974
Type Locality: Jacuhy River, at Cachoeira, Rio Grande do Sul, Brazil

besnardi Klappenbach, 1962. *Americuna* CRASSATELLIDAE
Boletim Instituto Oceanografico, Sao Paulo, 12(2):11, pl. 1
CM, 3 Paratypes, 60–88 (ex-MNHN, Montevideo)
MNHN, Holotype
Type Locality: Off Ubatuba (90 feet deep), Sao Paulo, Brazil

borealis Gray, 1882. *Unio* UNIONIDAE
Transactions of the Ottawa Field-Naturalists Club, 53, 3 figures
=*Lampsilis radiata* (Gmelin)
CM, 1 Paralectotype, 61.9926 (ex-Frierson from Latchford)
MCZ, Lectotype, 51470, selected by Johnson, 1956, Bulletin of the
Museum of Comparative Zoology
Type Locality: Ottawa River at Duck Island, Ottawa, Carleton Co.,
Ontario, Canada

brooksiana van der Schalie, 1938. *Anodonta* UNIONIDAE
Annals of Carnegie Museum, 27(12):167, p. 16, figs. 1–3
CM, Holotype and 234 Paratypes (coll. by Dr. and Mrs. S. T. Brooks),
MZUM, and “many museums,” Paratypes
Type Locality: Long Run Pond and Spout Pond Arm, Ferryland
Dist., South Shore, Newfoundland
See comments in Parodiz 1967, Sterkiana, 28:26

burkei Walker, 1922. *Quincuncina* UNIONIDAE
The Nautilus, 36:3, pl. 1, figs. 1–4 (in Ortmann and Walker)
CM, 1 Paratype (type-lot), 61.8622 (ex-Smith)
CM, 2 Paratypes (type-series), 61.8623 (ex-Burke), from Pea River,
5 mi. west of Elamville, Barbour Co., Alabama
MZUM, Holotype (from Walker coll. 41626)
Alabama State Museum, Paratypes
Type Locality: Sikes Creek, a tributary of Choctawatchee River,
Barbour Co., Alabama

caipira Ihering, 1893. *Unio* HYRIIDAE
Archiv für Naturgeschichte, 1:98
= probably a form of *Diplodon uruguayensis* (Lea) or hybrid of *D.*
uruguayensis × *expansus* (see Parodiz, 1968)
CM, 1 Paratype, 61.12979 (ex-Senckenberg Museum, 3875, from
Ihering)
Type Locality: Tanque Paraíso, Piracicaba, Sao Paulo, Brazil

- contraryensis* Utterback, 1916. *Quadrula quadrula* UNIONIDAE
American Midland Naturalist, 4 (Reprint):56, pl. 18, fig. 47
=*Quadrula quadrula* Rafinesque
CM, Neotype, 61.6892, here selected, and 2 Paratypes (ex-Utterback)
MCZ, 1 Paraneotype, 178926
Type Locality: Lake Contrary, at St. Joseph, Buchanan Co., Missouri
According to Johnson (1969, The Nautilus, 82(4):133), the "type" is lost ("none of the Utterback types have survived"). The neotype here selected corresponds to the measures of the second specimen of the four listed by Utterback, except that the length is 1 mm longer. The author mentioned a "sufficient coll." of this subspecies.
- coongoronta* Ortmann, 1912. *Lampsilis ventricosa* UNIONIDAE
The Nautilus, 26:53, not figured
=*Lampsilis ovata* Say
CM, Lectotype, male, 61.3994, selected by Parodiz, (Sterkiana, 1967).
Figured by Johnson, 1970, Bulletin of the Museum of Comparative Zoology, 140:pl. 21, fig. 1)
CM, Allotype, female, 61.4000, selected by Parodiz. (Figured by Johnson, idem. fig. 2)
CM, 9 Paralectotypes, 61.3999; 7, 61.5530; 9, 61.5965; 1, 61.5531
MCZ, 2 Paralectotypes, 273128
Type Locality: Potomac River at Hancock, Washington Co., Maryland
- cyclus* Pilsbry, 1901. *Petricola* PETRICOLIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53: 204
CM, 3 Syntypes, 61.9065 (ex-Hirase 1199)
ANSP, Syntypes, 80,580
Type Locality: Hirado, Hizen, Kyushu, Japan
- decipiens* Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 8:499, pl. 36, figs. 3-6; pl. 45, fig. 4; pl. 48, fig. 7; text fig. 4e
=*Diplodon martensi* (Ihering)
CM, Lectotype (Specimen #4: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.9253
CM, 7 Paralectotypes, 61.9253 (ex-Haseman)
Type Locality: A creek tributary of Iguazu River at Serrinha, State of Parana, Brazil
- deflexum* Sterki, 1922. *Pisidium* SPHAERIIDAE
Annals of Carnegie Museum, 13:429
=*Pisidium adamsi* Prime, according to Herrington, 1954
CM, 5 Syntypes, 9212a (ex-Berry)
Type Locality: Lake Winnecook, Unity, Maine
- dispar* Sterki, 1911. *Pisidium* SPHAERIIDAE
The Nautilus, 25(1):2
=*Pisidium casertanum* (Poli)

CM, 11 Syntypes, 6742 (ex-Smith; Walker)

Type Locality: Flood pools, 3 miles southwest of Evergreen, Alabama

enno Ortmann, 1921. *Diplodon* HYRIIDAE

Memoirs of Carnegie Museum, 8:531, pl. 38, fig. 5; pl. 46, fig. 7

=*Diplodon rotundus enno* (Ortmann)

CM, Lectotype (Specimen #1, female, single valve: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.9264

CM, 12 Paralectotypes, 61.9264

ANSP, Paralectotypes, 167875

Type Locality: Rio Grande, Boqueirao, Bahia, Brazil

ereganensis Grier, 1918. *Lasmigona costata* UNIONIDAE

The Nautilus, 32:(1):10

=*Lasmigona costata* (Rafinesque)

CM, Lectotype (selected by Parodiz, 1967) and 4 Paralectotypes, 61.4720 (ex-Ortmann)

CM, 8 Paralectotypes, 61.4223 (ex-Ortmann)

Type Locality: Big Bend (west of waterworks), Presque Isle Bay, Lake Erie, Erie Co., Pennsylvania

exile Sterki, 1916. *Pisidium abortivum* SPHAERIIDAE

Annals of Carnegie Museum, 10:3; 16:467

=*Pisidium insignae* Gabb

CM, 2 Syntypes, 10.007

Type Locality: Twin Lakes Swamp, Olga, Arcas Island, Washington

fimbriata Frierson, 1907. *Lampsilis* UNIONIDAE

The Nautilus, 21(8):86, pl. 12

=*Leptodea fimbriata* (Frierson)

CM, 1 Paratype (ex-Hinkley from Frierson), 61.4496

MZUM, Holotype, 87579, and 3 Paratypes, 167699

ANSP, Paratypes, 99547-9

Type Locality: Valles River, San Luis Potosi, Valles, Mexico

flucki Bartsch, 1906. *Nephronaias* UNIONIDAE

Proceedings of the United States National Museum, 30:393, pl. 17, fig. 2; pl. 13, fig. 2; pl. 19, figs. 1-2

=*Actinonaias flucki* (Bartsch)

CM, 2 Paratypes (ex-Fluck), 61.3953

USNM, Holotype, 106102

ANSP, Paratypes

Type Locality: Wounta River, Northwest of Kukallaya, Nicaragua

garbei Ihering, 1903. *Diplodon* HYRIIDAE

Senckenbergische naturforschende Gesellschaft, 32:133, pl. 12, figs. 7a-7b

=*Diplodon beskeanus* (Dunker)

CM, 2 Paratypes, 61.12984 (ex-Senckenberg Museum, from Ihering)

CM, 3 single valves, Paratypes, 61-52 (ex-MZUM, Walker collection)

Type Locality: Rio Doce, Lagoa Juparano, State of Espirito Santo, Brazil

- griseolum* Sterki, 1922. *Pisidium* SPHAERIIDAE
Annals of Carnegie Museum, 13:432
=*Pisidium casertanum* (Poli), according to Herrington, 1954
CM, 8 Syntypes, 9218 (ex-Berry)
Type Locality: Lake Wianecook, Unity, Maine
- hartwrighti* Ihering, 1910. *Diplodon* HYRIIDAE
über Brasilianischen Najaden, Abhandlung, Senckenbergische naturforschende Gesellschaft, 32:11–40
=*Diplodon rhombeus* (Wagner in Spix), see Parodiz, 1968
CM, 2 Paratypes, 61.12981 (ex-Senckenberg Museum, 3925, from Ihering)
Type Locality: Lagoa Alagadinha, Goias, Brazil
- hasemani* Ortmann, 1921. *Anodontites* MYCETOPODIDAE
Memoirs of Carnegie Museum, 8:609
CM, Lectotype (Specimen #3: selected by Bonetto, 1959, subsequent designation by Parodiz, 1968), and 3 Paralectotypes, 61.5832 (ex-Haseman)
Type Locality: Headwaters of Rio Paraguay, Santa Rita, Matto Grosso, Brazil
- hasemani* Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 8:478, pl. 34, figs. 1, 4; pl. 47, fig. 5; text fig. 4a
=*Diplodon guaranianus* (d'Orbigny)
CM, Lectotype (Specimen #10: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.5857
CM, 8 Paralectotypes, 61.5857 (ex-Haseman)
MCZ, 1 Paralectotype, 47040
ANSP, 1 Paralectotype, 167869
Type Locality: Rio Guapore, near Rio Sao Simao, Matto Grosso, Brazil
- hildae* Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 8:514, pl. 36, figs. 1–2; pl. 46, fig. 3
=*Diplodon piceus* (Lea), see Parodiz 1968, Sterkiana, 30:12
CM, Lectotype (Specimen #15: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.5864
CM, 8 Paralectotypes, 61.5864 (ex-Haseman)
ANSP, 1 Paralectotype, 167911
Type Locality: Rio Jacuhy at Cachoeira (100 miles west of Porto Alegre), Rio Grande do Sul, Brazil, coll. Haseman, 26 January 1905
- hollandi* Ortmann, 1921. *Monocondylaea* MYCETOPODIDAE
Memoirs of Carnegie Museum, 8:585
CM, Holotype (by monotypy), 61.5846 (ex-Haseman)
Type Locality: Rio Guapore, nr. Rio Sao Simao, Matto Grosso, Brazil
- hyroides* Ortmann, 1921 *Anodontites* MYCETOPODIDAE
Memoirs of Carnegie Museum, 8:604
=*Anodontites trigonus* (Spix), cf. Haas, 1931

CM, Lectotype (Specimen #6: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), and 5 Paralectotypes, 61.5829 (ex-Haseman)

Type Locality: Rio Tapajos, Santarem, Para, Brazil

imitator Ortmann, 1921. **Diplodon** HYRIIDAE

Memoirs of Carnegie Museum, 8:491, pl. 34, figs. 5–7; pl. 45, figs. 1, 2; pl. 47, fig. 6

=**Diplodon martensi** (Ihering)

CM, Lectotype (Specimen #29: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.9248

CM, 21 Paralectotypes, 61.9248 and 61.9249 (ex-Haseman)

Type Locality: Vaccahy-Mirim River, Santa Maria, Rio Grande do Sul, Brazil

infossus H. B. Baker, 1930. **Anodontites** MYCETOPODIDAE

Occasional Papers, Museum of Zoology, University of Michigan, 210:67

CM, 1 Paratype, 61-97 (ex-MZUM)

MZUM, Holotype, 112621

ANSP, Paratype, 147132

Type Locality: Cano Minopan, (tributary of Rio Aroa), near Palma Sala, Venezuela

iridella Pilsbry and Frierson, 1908. **Lampsilis** UNIONIDAE

The Nautilus, 22(8):81 (figs. in volume 21, pl. 12, 1907)

=**Villosa (Friersonia) iridella** (Pilsbry and Frierson)

CM, 3 Paratypes (ex-Hinkley)

ANSP, Holotype, 93810a

MCZ, 3 Paratypes, 100405

Hinkley and Frierson Coll., Paratypes

Type Locality: Valles River, San Luis Potosi, Mexico

kamerunensis Walker, 1910. **Spatha** MUTELIDAE

The Nautilus, 24, 38, pl. 3, figs. 1–2

CM, 1 Paratype, 61.4489 (ex-Walker from Schwab)

MZUM, Holotype, 30902, plus Paratypes

ANSP, 1 Paratype, 101287

Museum d'Histoire Naturelle, Paris (coll. Germain), 1 Paratype

Type Locality: Kribi River, 17 miles from Efulen, Cameroon, Africa

kelseyi F. C. Baker, 1913. **Diplodon** HYRIIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 65: 618–672, pl. 27, figs. 6–7

CM, 1 Paratype, 61–63, (ex-MZUM, Walker coll.)

ANSP, Figured Holotype, 109371

Type Locality: Rio Jamauchim, Lat. 5°30'S., Long. 54°15'W, Brazil

kirklandi Sterki, 1899. **Pisidium** SPHAERIIDAE

The Nautilus, 13:11

=**Pisidium fallax** Sterki

CM, 30 Syntypes, 2643 (ex-Kirkland) “over 200 specimens”

Type Locality: Grand River, Grand Rapids, Michigan

- kiusiuensis* Pilsbry, 1901. *Donax* DONACIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53:
207, 400, pl. 20, fig. 29
CM, 6 Syntypes, 61.9074 (ex-Hirase 847, and ANSP 80,505)
Type Locality: Hirado, Hizen, Kyushu, Japan
- lananensis* Frierson, 1901. *Quadrula* UNIONIDAE
The Nautilus, 15:75, pl. 4
=*Fusconaia lananensis* (Frierson)
CM, 2 Paralectotypes (ex-Askew, Strode and Frierson, from Frierson
coll.), 61.5006
ANSP, Lectotype, 81561a, and Paralectotypes, 81561
MCZ, Paralectotypes, 69757
USNM, Paralectotypes
Askew and Strode coll., Paralectotypes
Type Locality: Lanana Creek, Nacogdoches, Nacogdoches Co., Texas
- leucogona* Ortmann, 1913. *Fusconaia subrotunda* UNIONIDAE
The Nautilus, 27:89 (not figured)
=*Fusconaia subrotunda* (Lea)
CM, Lectotype and 9 Paralectotypes, 61.5239 (ex-Ortmann), se-
lected by Parodiz, 1967, Sterkiana, 28:23 (figured by Johnson,
1977, Occasional Papers, Museum of Comparative Zoology, 4:
pl. 27, fig. 2)
OSM, 1 Paralectotype
MCZ, 1 Paralectotype, No. B
Type locality: Elk River, Gassaway, Braxton Co., West Virginia
- limosa* Maton, 1809. *Tellina* CORBICULIDAE
Transactions of the Linnean Society, London, 10:325, figs. 8–10.
Neotype described in Annals of Carnegie Museum, 1965, 38(3);80,
fig. 9 a–i
=*Neocorbicula limosa* (Maton, 1809)
=*Cyrena variegata* d'Orbigny, 1835. Magasin de Zoology (Paris),
p. 37
CM, Neotype and 5 Paraneotypes, 61262, Parodiz and Hennings,
1965
Type Locality: Arroyo las Piedras (for Neotype), Prov. Buenos Aires,
Argentina, collected by Parodiz, 1961
- lithura* Pilsbry, 1905. *Lithophaga* MYTILIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 57:
119, pl. 5, figs. 37–39
CM, 5 Syntypes, 61.9405 (ex-Hirase 1577)
ANSP, Syntypes, 88,294 (from 1577 of Hirase's collection)
Type Locality: Kikaigashima, Osumi, Kyushu, Japan
- mainense* Sterki, 1903. *Pisidium walkeri* var. SPHAERIIDAE
The Nautilus, 12:79
=*Pisidium mainense* Sterki (The Nautilus, 17(1):21)
CM, 18 Syntypes (of type-series), 2356 (ex-Nylander)
Type Locality: "several places in Aroostook Co., Maine, by O.O.
Nylander"

- martensi* Ihering, 1893. *Castalina* HYRIIDAE
Archiv für Naturgeschichte, 81
See Ortmann, Memoirs of Carnegie Museum, 8:551
CM, 5 Paratypes, 61.11127 (ex-Sterki from Ihering)—“Ihering’s original label”
CM, 2 Paratypes, 61.12982 (ex-Senckenberg Museum, from Ihering)
Type Locality: Rio Camaquã, Rio Grande do Sul, Brazil
- mediamericana* Pilsbry, 1919. *Donax* DONACIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, (1920), 71:222, pl. 11, fig. 10
CM, 39 Syntypes, 61.7930 (ex-Hinkley, and ANSP)
Type Locality: Beach, Livingston, Guatemala
- mogymirim* Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 520, pl. 37, figs. 4–7; pl. 46, fig. 5; pl. 48, fig. 2
=*Diplodon expansus* (Küster)
CM, Lectotype (No. 22); Allotype (No. 38); 12 Paratypes, 61.9260), subsequent designation by Parodiz, 1968
CM, 9 Paralectotypes, 61.9261
CM, 72 Paralectotypes, 61.9262
ANSP, 1 Paralectotype
Type Locality: Creek near Mogy-Mirim, São Paulo, Brazil
- nehringi* Ihering, 1893. *Castalina* HYRIIDAE
Archiv für Naturgeschichte, 75; See Ortmann, Memoirs of Carnegie Museum, 8, 1921, 548
CM, 2 Paratypes, 61.5118 (ex-Haseman from Ihering)
CM, 1 Paratype, 61.12983 (ex-Senckenberg Museum, from Ihering)
Type Locality: Rio Piracicaba, São Paulo, Brazil
- obesa* Ortmann, 1921. *Monocondylaea* MYCETOPODIDAE
Memoirs of Carnegie Museum, 8:583, pl. 9, fig. 4
CM, Lectotype (Specimen #10: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.5850
CM, 10 Paralectotypes, 61.5850 (ex-Haseman)
Type Locality: Rio Tapajós, Santarém, Pará, Brazil
- ortmanni* Frierson, 1913. *Unio* (*Nephronaias*) UNIONIDAE
The Nautilus, 27:14; 28, pl. 2
=*Actinonaias calamitarum ortmanni* (Frierson)
CM, 24 Paralectotypes, 61.6196 (ex-Hinkley)
ANSP, Lectotype, 117544a (selected by Johnson, 1972)
MCZ, 3 Paralectotypes, 20916
Type Locality: Rio Conchins, Maya Farm, Quirigua, Guatemala
- oscari* Wright, 1892. *Unio* UNIONIDAE
The Nautilus, 5:124; 1895, 19:122, p. 2, fig. 3
=*Elliptio productus* (Conrad)
CM, 1 Paratype, 61.11808 (ex-Walker from Daniels coll.)
ANSP, Holotype
Type Locality: Lake Osceola, Winter Park, Orange Co., Florida

- parodizi* Bonetto, 1961. *Diplodon* HYRIIDAE
 Primera Reunión Trabajos Ciencias Naturales del Litoral, Volume 1, pp. 214–219. Universidad Nacional del Litoral, Santa Fe, Argentina.
 This is the species figured by Sowerby (in Reeve's Conchologia Iconica, vol. 1, sp. 169-1868) as *Unio burroughianus* (not *burroughianus* Lea)
 CM, 16 Paratypes, 52-1 (ex-Bonetto), plus other lots from different localities identified by the author of the species
 Instituto Nacional de Limnología, Santa Fe, Argentina, Holotype ANSP, 1 Paratype
 Type Locality: Laguna Vargas, at the confluence of Arroyo Malabrigo and San Javier Riv., near Romang, Santa Fe, Argentina
- parvula* Grier, 1918. *Fusconaia flava* UNIONIDAE
 The Nautilus, 32:11 (Not figured)
 The Nautilus, 1919:21, pl. 2, fig. 2 (Ortmann)
 =*Fusconaia flava* Rafinesque
 CM, Lectotype, selected by Parodiz, 1967, (Ortmann, fig. 2), and 15 Paratypes, 61.4513
 CM, 5 Paralectotypes, 61.2886 (ex-Ortmann)
 CM, 1 Paralectotype, 61.4370 (ex-Ortmann), from "South shore" of type locality
 Type Locality: Big Bend, Presque Isle Bay, Erie, Erie Co., Pa.
 Collected by Ortmann, 8 July 1910
- paulista* Ihering, 1893. *Unio* HYRIIDAE
 Najaden von Sao Paulo, Archiv für Naturgeschichte, 1:45–140, p. 93, pl. 4, fig. 7
 =*Diplodon delodontus expansus* (Küster)
 CM, 2 Paratypes, 61.12980 (ex-Senckenberg Museum, from Ihering)
 CM, 1 Paratype, 61-94 (ex-MZUM)
 Type Locality: Piracicaba, Tiete River, Sao Paulo, Brazil
- peraltum* Sterki, 1900. *Pisidium* SPHAERIIDAE
 The Nautilus, 14:5
 CM, 52 Syntypes, 46917 (ex-Sterki from Kirkland)
 National Museum of Victoria, Melbourne, Australia, Syntypes
 Type Locality: Crystal Lake, Menzie Co., Michigan
- phenax* Pilsbry, 1901. *Paphia (Tapes)* VENERIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53: 207, p. 400, pl. 19, fig. 5
 =*Tapes phenax* Pilsbry (as named in illustration)
 CM, 4 Syntypes, 61.9064 (ex-Hirase 432B)
 ANSP, Syntypes, 80,436
 Type Locality: "Loochoo Islands" (=Ryukyu Islands, Okinawa Prefecture), Japan
- pilula* Sterki, 1922. *Pisidium* SPHAERIIDAE
 Annals of Carnegie Museum, 13:437
 =*Pisidium ferruginosus* Prime

CM, 1 Syntype, 9261 (ex-Hanham)

Type Locality: Small swamp, Anamchan, Vancouver Isl., British Columbia

riograndensis Ihering, 1890. *Anodontites* MYCETOPODIDAE

Archiv für Naturgeschichte, 154

See: Ortmann, Memoirs of Carnegie Museum, 8:624

=*Anodontites trapezialis forbesianus* (Lea), cf. Mansur, 1970

Senckenberg Museum: "Type" 3838

CM, 8 Paratypes, 61.11134 (ex-Sterki from Ihering)—"original label in Ihering's handwriting" (Brooks), from Rio Camaquã, Rio Grande do Sul, Brazil

CM, 3 Paratypes, 61.12986 (ex-Senckenberg Museum, from Ihering), from Rio Guahyba, St. Rio Grande do Sul, Brazil

Type Locality: Rio Grande do Sul, Brazil

roseomaculatus Pilsbry, 1901. *Solen* SOLENIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53: 399, pl. 19, fig. 13

CM, 3 Syntypes, 61.9076 (ex-Hirase 1044)

ANSP, Syntypes, 80,565

Type Locality: Hirado, Hizen, Kyushu, Japan

santanus Ihering, 1910. *Diplodon ellipticus* HYRIIDAE

über Brasilianischen Najaden, Abhandlung, Senckenbergische naturforschende Gesellschaft, (134)32:11–40. Type figure in Haas, 1931, fig. 19

=*Diplodon rhombeus* (Wagner), see Parodiz, 1968

CM, 1 Paratype, 61.12985 (ex-Senckenberg Museum, 3894, from Ihering)

Type Locality: Rio Santa Maria, Espirito Santo, drainage of Dolce River, Brazil

selecta Wheeler, 1914. *Fusconaia* UNIONIDAE

The Nautilus, 28:75, pl. 5

=*Fusconaia flava* (Rafinesque)

CM, 2 Paratypes, 61.7723 (ex-Wheeler from Frierson)

Wheeler coll., Holotype

ALA, Paratypes

ANSP, "Type"

Type Locality: Cache River, Nemo, Craighead Co., Arkansas

simillimus Ortmann, 1921. *Diplodon* HYRIIDAE

Memoirs of Carnegie Museum, 8:495, pl. 35, figs. 3–6; pl. 45, fig. 2

=*Diplodon martensi* (Ihering)

CM, Lectotype (Specimen #22: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.9250

CM, 26 Paralectotypes, 61.9250 (ex-Haseman)

MCZ, 2 Paralectotypes, 47050

ANSP, Paralectotype, 167907

Type Locality: Nhundiaquora River, at Morretes, State of Parana, Brazil

- sinuosum* Morrison, 1943. *Guianadesma* CORBICULIDAE
The Nautilus, 57(2), p. 49, Oct. 1943, pl. 8, fig. 1; figs. 2–6
= *Ostomya fluviatilis* H. Adams
CM, 14 Paratypes, 46763 (ex-Morrison and Benkert), 39
USNM, Holotype and Paratypes, 536901
Type Locality: from rocks in the midstream of Cuyuni River, opposite Kartabo Point, near junction with the Mazaruni River, Essequibo District, British Guiana
- stelzneri* Parodiz, 1969. *Neocorbicula* CORBICULIDAE
Annals of Carnegie Museum, 40:93, pl. 11, figs. 2, 3
CM, 30 Paratypes, 45435 (ex-Herbst)
Instituto Lillo of Tucuman, Holotype and 150 Paratypes
Type Locality: east of Santa Maria, in the Santa Maria Valley west of Sierra Aconquija (near limit with Tucuman), Prov. Catamarca, Argentina (Calchaqui Beds), mid-Miocene.
- sterkii* Grier, 1918. *Elliptio dilatatus* UNIONIDAE
The Nautilus, 32:9
= *Elliptio dilatatus dilatatus* (Rafinesque)
CM, Lectotype (selected by Parodiz, 1967), and 9 Paralectotypes (figured in Ortmann, 1909, Annals of Carnegie Museum, 5:pl. 8, fig. 3)
Type Locality: Big Bend (west of waterworks), Presque Isle, Erie Co., Pennsylvania, coll. Ortmann, 1910
- strengii* Sterki, 1902. *Pisidium* SPHAERIIDAE
The Nautilus, 15:126
CM, 63 Syntypes, 46918 (ex-Sterki from Kirkland)
National Museum of Victoria, Melbourne, Australia, Syntypes
Type Locality: Perch Lake, Kent Co., Michigan and Reed Lake, Michigan (Daniels, collector)
- subinflata* Anthony, 1865. *Anodonta* UNIONIDAE
American Journal of Conchology, 1:160, pl. 15, fig. 1
= *Anodonta grandis* Say
CM, 2 Paratypes, 1954–5 (ex-MCZ)
MCZ, Holotype, 161863
Type Locality: Shears Lake, Kent Co., Michigan
- succineum* Sterki, 1907. *Pisidium* SPHAERIIDAE
The Nautilus, 20(9):99
= *Pisidium casertanum* (Poli)
CM, 105 Syntypes (of type-series), 616 (ex-Sterki)
Type Locality: “common e.g. in vicinity of Washington, D.C., and Alexandria, Virginia, where it was collected in 1896 by the writer—”, etc. The type locality must be New Philadelphia, Ohio
- transandinus* Parodiz, 1963. *Diplodon* HYRIIDAE
New Fresh-water Mollusks from the Eocene of Chile and Patagonia, The Nautilus, 76:145–147, p. 145, pl. 2, figs. 1–4
CM, Holotype, 46800 (ex-Porter coll.; Thomas collector)
Type Locality: At Paso Tinguirica, Jahuel Formation, between headwaters of the Tinguirica and Grande rivers, Colchagua, Chile, Paleocene

- vicarius* Ortmann, 1921. *Diplodon* HYRIIDAE
Memoirs of Carnegie Museum, 8:497, pl. 25, figs. 7–8; pl. 34, figs 1, 2; pl. 45, fig. 3
=*Diplodon martensi* (Ihering)
CM, Lectotype (Specimen #15: selected by Bonetto, 1959; subsequent designation by Parodiz, 1968), 61.9251
CM, 10 Paralectotypes, 61.9251 (ex-Haseman)
Type Locality: Aqua Quente, Ipiranga, Sao Paulo, Brazil, in creeks, tributaries of Ribeira River
- walkeri* Wilson and Clark, 1914. *Truncilla* UNIONIDAE
Bureau of Fisheries, Document 781:46
See Ortmann, Proceedings of the American Philosophical Society, 57, 1918, 591
=*Dysnomia walkeri* (Wilson and Clark)
CM, 4 Paratypes, 61.6769 (ex-Walker from Wilson and Clark)
Type Locality: East Fork of Stones River, Walterhill, Rutherford Co., Tennessee
- waltoni* Wright, 1888. *Elliptio* UNIONIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 40: 114, pl. 2, fig. 3
=*Elliptio productus* (Conrad)
CM, 1 Paratype, 61.11835 (ex-Walker from Daniels, 500)
ANSP, Holotype
MCZ, Paratypes, 167701
Type Locality: Lake Woodruff, central E. Florida, Volusia Co., Florida
- wheeleri* Ortmann and Walker, 1912. *Arkansia* UNIONIDAE
The Nautilus, 25(9):98, pl. 8
CM, 1 Syntype, 61.5357 (ex-Wheeler)—“Third specimen found”
CM, 2 Syntypes, 61.5358 (ex-Wheeler)
MCZ, 2 Syntypes, 135712 and 12219
MZUM, Walker Collection, Syntypes (33754)
Type Locality: “Old River,” cf. Ouachita River, Arkadelphia, Clark Co., Alabama

Gastropoda

Prosobranchia

- acuta* Geyer, 1904. *Vitrella quenstedti* form HYDROBIIDAE
 Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1904:312.
 =*Bythiospeum quenstedti* (Wiedersheim)
 CM, 1 Paratype, 62.16764 (ex-Blume)
 SMF, Lectotype, Paratypes
 Type Locality: Elsachquelle, near Urach, Württemberg, Germany
- alba* Pilsbry, 1903. *Pupinella rufa* form CYCLOPHORIDAE
 Catalog of the Land Shells of Japan, 21—see The Nautilus, 45(1931):29
 CM, 6 Paratypes, 62.15733 (ex-Hirase 731b)
 ANSP, Holotype and Paratypes, 82268
 Type Locality: Hirado, Hizen, Kyushu, Japan
- albescens* Hartman, 1890. *Helicina* HELICINIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 42: 285, pl. 3, fig. 5
 =*Pleuropoma albescens* (Hartman)
 CM, Holotype, 62.15313
 Type Locality: Segou Island, New Hebrides
- altior* Pilsbry, 1892. *Vivipara georgiana* VIVIPARIDAE
 The Nautilus, 5:142
 =*Viviparus georgianus* (Lea)
 CM, 17 Paralectotypes, 62.7023 (ex-Pilsbry)
 ANSP, Lectotype, 63420 (selected by H. B. Baker, 1964)
 Type Locality: Aboriginal shell-heap, left bank of Hitchen's Creek, near entrance of St. John's River into Lake George, Florida
- ampla* Pilsbry, 1902. *Diplommatina kobelti* var. CYCLOPHORIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 54:28
 CM, 6 Syntypes, 62.15474 (ex-Hirase 812)
 ANSP, Syntypes, 82,664 from Hirase 812
 Type Locality: Goto, Uzen (Yamagata Prefecture), Honshu, Japan
- angulatus* Pilsbry, 1901. *Cyclophorus turgidus* var. CYCLOPHORIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:549
 CM, 4 Syntypes, 62.15459 (ex-Hirase coll. 713)
 Type Locality: "Loo Choo" (=Ryukyu Islands, Okinawa Prefecture), Japan
- apreitensis* H. B. Baker, 1924. *Tudora megacheilos* CHONDROPOMIDAE
 Occasional Papers, Museum of Zoology, University of Michigan, 152:58
 =*Licina megacheilos apreitensis* (H. B. Baker), NEW COMBINATION
 CM, 10 Paratypes, 62.26812 (ex-Goodrich)
 MZUM, Holotype
 Type Locality: Base of northern escarpment, Seroe Spreit, Curacao, Dutch Leeward Islands

- ara* Geyer, 1905. *Vitrella quenstedti* var. HYDROBIIDAE
 Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1905:295
 = *Bythiospeum quenstedti* (Wiedersheim)
 CM, 2 Paratypes, 62.16765 (ex-Blume)
 SMF, Lectotype, Paratypes
 Type Locality: Reissenbaches, near Reutlingen, Württemberg, Germany
- arata* Pilsbry, 1902. *Helicina yoshiwarana* HELICINIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 54:26
 CM, 6 Syntypes, 62.15648 (ex-Hirase 857)
 Type Locality: Agawara-jima, Bonin Islands, Japan
- articulata* Pilsbry, 1901. *Daphnella fragilis* TURRIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:385, pl. 21, fig. 26
 CM, 4 Syntypes, 62.9987 (ex-Hirase 903)
 ANSP, "Types," 80,634
 Type Locality: Hirado, Hizen, Kyushu, Japan
- arubana* H. B. Baker, 1924. *Tudora fossor* CHONDROPOMIDAE
 Occasional Papers, Museum of Zoology, University of Michigan, 152:68
 = *Licina fossor arubana* (H. B. Baker), NEW COMBINATION
 CM, 7 Paratypes, 62.26814 (ex-Goodrich)
 MZUM, Holotype
 Type Locality: Spur of Seroe Pretoe, between Roois Spoki and Hundae, Southern Aruba, Dutch Leeward Islands
- aurantiaca* Torre. *Eutrochatella chrysoschasma* HELICINIDAE
 Reference and year of publication unknown.
 CM, 6 presumed Paratypes 62.26788 (ex-Jaume, 1933)
 Type Locality: Coco Solo, Viñales, Pinar del Rio, Cuba. The Type is probably at the University of Havana.
- aureo-labris* Simpson (in Henderson), 1894. *Adamsiella grayana* var. CHONDROPOMIDAE
 The Nautilus, 8:23 (short diagnosis)
 = *Adamsiella grayana* Pfeiffer
 CM, 1 Syntype, 62.38660
 UCM, Syntypes, 172, ex-Henderson coll.
 Type Locality: Rio Novo, Jamaica
- awaensis* Pilsbry and Hirase, 1904. *Alycaeus* CYCLOPHORIDAE
 The Nautilus, 17:117
 CM, 6 Syntypes, 62.15432 (ex-Hirase 1083)
 ANSP, Syntypes, 84958, from 1083 of Hirase coll.
 Type Locality: Hiayama, Awa (Tokushima Prefecture), Shikoku, Japan
- bacillum* Pilsbry, 1901. *Syrnola* PYRAMIDELLIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:394, pl. 21, fig. 25
 CM, 3 Syntypes, 62.9900 (ex-Hirase 1239)

ANSP, "Types," 80,605, from Hirase 1,239

Type Locality: Hirado, Hizen, Kyushu, Japan

bermudezi Torre and Bartsch, 1938. *Turritrypa* (*Turripoma*)

CHONDROPOMIDAE

Proceedings of the United States National Museum, 85:251, pl. 13, fig. 2

CM, 2 Paratypes, 62.26787 (ex-Jaume)

USNM, Holotype, 367904 (ex-Bermudez)

Type Locality: On palms, Cueva del Carte, Sierra del Paso Real de Guanc, Cuba

bicolor Gould, 1842. *Cyclostoma*

POMATIASIDAE

Proceedings of the Boston Society of Natural History, 4(1):452

=*Megalomastoma* (*Farcimen*) *auriculata* (d'Orbigny)

CM, 6 Syntypes, 62.26805 (ex-Bartlett from Clench, MCZ)

Type Locality: Cuba

biexcisus Pilsbry, 1902. *Alycaeus*

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54:26

CM, 6 Syntypes, 62.15428 (ex-Hirase)

ANSP, Syntypes, 82,660 from 831b of Hirase

Type Locality: Suimara, Awa (Tokushima Prefecture), Shikoku, Japan

bitaeniata Hartman, 1890. *Helicina*

HELICINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 42: 286, pl. 3, fig. 10

CM, 4 Syntypes, 62.39825

Type Locality: Dominique, Marquesa Islands

boultoni Bequeart and Clench. *Viviparus* (*Bellamya*)

VIVIPARIDAE

in litteris, according to Clench

CM, 1 Paratype, 62.32346 (ex-Boulton, Pulitzer Exped.)

MCZ, Holotype

Type Locality: Cumene River, Caleneque, Angola, Africa

brandi Drake, 1953. *Amnicola*

HYDROBIIDAE

Journal of the Washington Academy of Science, 43:26, figs. 1-6

CM, 8 Paratypes, 62.39827 (ex-Drake and Hoff)

Type Locality: Warm Springs, Las Palomas, Distrito Caleana, Chihuahua, Mexico

brownii Carpenter, 1872. *Lyogyrus*

HYDROBIIDAE

Central Fall Weekly Visitor, Central Falls, Rhode Island (April 1872) (Pilsbry, H. B. Baker, and other informed authors reported that they have not seen this paper.)

CM, 2 Paralectotypes, 62.40536 (ex-Miller)

ANSP, Lectotype, 27816 (H. B. Baker, 1964)

Type Locality: Providence, Providence Co., Rhode Island

cacaguelita Pilsbry and Clapp, 1902. *Helicina*

HELICINIDAE

The Nautilus, 15:136, 137, pl. 7, fig. 6

CM, 2 Syntypes, 46759 (ex-Smith from Clapp 4538)

ANSP, Syntypes

Type Locality: Santa Marta Mts., Colombia, at Cacagualito, 1500'

- callipeplum* Bartsch. *Chondropoma* CHONDROPOMIDAE
Reference unknown. (Listed by Fluck, The Nautilus, 20(1):4, 1906.)
This may be a *nomen nudum*.
CM, 3 "Types" (on label), 62.7646 (ex-Fluck)
Type Locality: Wani, Nicaragua
- caribaea* Clench and Aguayo, 1935. *Poteria* CYCLOPHORIDAE
The Nautilus, 49:51
CM, 7 Paratypes, 62.26828 (ex-Clench from Arnold)
MCZ, Holotype, 109264
ANSP, MZUM, and Aguayo coll., Paratypes
Type Locality: Spring Mount, St. James, Jamaica
- caribbea* Rehder, 1943. *Rissoella* (*Phycodrosus*) RISSOELLIDAE
Proceedings of the United States National Museum, 93:194, pl. 20,
fig. 7
(*Phycodrosus* Rehder, 1943 = *Rissoella sensu stricto*)
CM, 3 Paratypes, 62.40552 (ex-Bales)
USNM, Holotype (not in Richard and Old's Catalog, 1969)
Type Locality: Bonefish Key, Florida
- caribbaeum* Clapp, 1914. *Chondropoma* CHONDROPOMIDAE
The Nautilus, 27:100
CM, 1 Syntype, 46772 (ex-Nelson)
MCZ, Syntypes, 22885
Type Locality: Swan Island, Caribbean Sea
- cassa* Pilsbry, 1901. *Diplommatina* CYCLOPHORIDAE
The Nautilus, 15:23
CM, 24 Syntypes, 62.15620 (ex-Hirase 604)
Type Locality: Kodakari, Prov. Hida (Gifu Prefecture) and Kyoto,
Honshu, Japan
- chalarogyrus* Thompson, 1968. *Aphaostracon* HYDROBIIDAE
Hydrobiidae of Florida (University of Florida Press), 97, figs. 54 G–
K and 64 F–G
CM, 188 Paratypes, 65–13 (ex-Thompson)
MZUM, Holotype, 215515
MZUM, 400 Paratypes, 216516
USNM, 100 Paratypes, 636942
MCZ, 100 Paratypes, 258007
ANSP, 100 Paratypes, 301547
Type Locality: Magnesia Springs, 3.7 miles west of Hawthorne, Ala-
chua Co., Florida
- cheatumi* Pilsbry, 1935. *Potamopyrgus* HYDROBIIDAE
The Nautilus, 48:91, fig. 4
= *Lyrodes cheatumi* (Pilsbry), NEW COMBINATION
CM, 25 Syntypes, 46757 (ex-Cheatum)
ANSP, Syntypes, 163888
Type Locality: Phantom Lake, near Tayahvale, Reeves Co., Texas
- chemnitzianus* Pilsbry, 1901. *Cerithium* CERITHIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53:
393, pl. 19, figs. 14–15

CM, 6 Syntypes, 62.9923 (ex-Hirase) Hirase coll.

ANSP, Syntypes

Type Locality: "Loo Choo Islands" (=Ryukyu Islands, Okinawa Prefecture), Japan

chocoloccoensis Smith, 1922. *Anculosa* PLEUROCERIDAE

In Goodrich, Miscellaneous Publications, Museum of Zoology, University of Michigan, 7:34, pl. 1, fig. 7; pl. 3, fig. 14

CM, 5 Paratypes, 62.17476 (ex-Clapp from Smith)

ALA, Paratypes

MZUM, Holotype

Type Locality: Jackson Shoals, Choccolocco Creek, Talladega Co., Alabama (coll. Smith, 1905)

cisternina Walker, 1919. *Amnicola* HYDROBIIDAE

Occasional Papers, Museum of Zoology, University of Michigan, 73:1, pl. 1, fig. 1

CM, 100 Syntypes, 62.16423 (ex-Hinkley)

MZUM, Syntypes (ex-Walker coll. 47161)

Type Locality: Reservoir, 4 miles north of Guatemala City, Guatemala

clappi Pilsbry, 1909. *Helicina orbiculata* HELICINIDAE

The Nautilus, 23:90

=*Helicina clappi* Pilsbry

CM, 3 Paralectotypes, 46761 (ex-Rhoads)

ANSP, Lectotype, 77065 (ex-Pilsbry and Rhoads coll. 1899), selected by Pilsbry in 1948 from the originally described "syntypes"

Type Locality: Miami, Dade Co., Florida

claudicans Poey, 1858. *Cyclostoma* CHONDROPOMIDAE

Memorias sobre la Historia Natural de la Isla de Cuba, 2:43, pl. 2, fig. 8

=*Chondrothyrella (Plicathyrella) claudicans* (Poey), NEW COMBINATION

CM, 5 "Topotypes," 62.28910 (ex-Aguayo)

University of Havana, "Type"

USNM, "specimen" 492733

Type Locality: Rangel, Pinar del Rio, Cuba

clenchii Goodrich and Van der Schalie, 1937. *Somatogyrus* HYDROBIIDAE

Miscellaneous Publications, Museum of Zoology, University of Michigan, 34:pl. 1, fig. 1

CM, 5 Paratypes, 62.29081 (ex-Goodrich)

MZUM, Holotype

Type Locality: Pasion River, at Sayanche, Dept. Peten, Guatemala

clipeata Smith, 1922. *Anculosa* PLEUROCERIDAE

In Goodrich, Miscellaneous Publication, Museum of Zoology, University of Michigan, 7:19, pl. 1, figs. 8-10; pl. 3, fig. 8*

* Note: A simultaneous "publication" of Smith's (in Goodrich) *Anculosa* 1922 was made by the Geological Survey of Alabama, Alabama Museum Paper No. 6; it is a reprint of the original publication from Michigan with a different cover.

CM, 17 Paratypes, 62.17421 (ex-Clapp from Smith)

MZUM, Holotype

ALA, Paratypes

Type Locality: Ft. William Shoals, Coosa River, Shelby Co., Alabama (coll. Smith, 1914)

conchensis Walker, 1919. *Amnicola* HYDROBIIDAE
Occasional Papers, Museum of Zoology, University of Michigan, 73:3, pl. 1, figs. 4–5

CM, 97 Paratypes, 62.16425 (ex-Hinkley)

MZUM, "Type" (ex-Walker coll. 38505, fig. 5)

Type Locality: Conchins River, Maya Farm, Quirigua, Guatemala

concinna Godwin-Austen, 1892. *Diplommatina* CYCLOPHORIDAE
(*non* H. Adams, 1872)

Proceedings of the Zoological Society, London, 519

=*Diplommatina godwini* Möllendorf, 1898

CM, 2 Syntypes, 46766 (ex-Doherty and ex-Aldrich)

Type Locality: E. Naga Hills, South of Margarita, India

concordianus Parodiz, 1966. *Potamolithus felipponei* HYDROBIIDAE
The Nautilus, 80:57, pl. 4, figs. 5–6
CM, Holotype and 3 Paratypes, 43–159 (ex-Parodiz)
Type Locality: Arroyo Yuqueri Grande, at Concordia, Entre Rios, Argentina

cotabatoensis Bartsch, 1919. *Leptopoma* CYCLOPHORIDAE
Proceedings of the Biological Society of Washington, 32:18–19
=*Leptopoma goniostoma cotabatensis* (Bartsch), (*fide* MacMillan)
CM, 1 Paratype, 62.29549 (ex-Eyerdam)
Type Locality: Kidapayan, Cotabato, Mindanao, Philippine Islands

cozumelense Richards, 1937. *Choanopoma* CHONDROPOMIDAE
Proceedings of the American Philosophical Society, 77:256, pl. 4, fig. 3
=*Annularia cozumelensis* (Richards)
CM, 17 Syntypes (ex-Richards), 62.33057
ANSP, Syntypes, 167749
Type Locality: San Miguel, Cozumel, Mexico

crassa Thompson, 1968. *Onobops* HYDROBIIDAE
Hydrobiidae of Florida (University of Florida Press), 32, figs. 50 I–J, 58 E
CM, 5 Paratypes, 65012 (ex-Thompson)
MZUM, Holotype 216537, and 133 Paratypes, 216538
USNM, 5 Paratypes, 636947
ANSP, 5 Paratypes, 301539
MCZ, 5 Paratypes, 258005
UF, Paratypes
Type Locality: Mangrove marsh, 1.9 miles north Everglades, Collier Co., Florida

dalli Bartsch. *Helicina* HELICINIDAE
No reference known. (Listed by Fluck, The Nautilus, 20(1):4, 1906).
This may be a *nomen nudum*.

CM, 2 Syntypes, 62.7645 (ex-Fluck)
Type Locality: Wani, N. E. Nicaragua

decipiens Walker, 1909. ***Somatogyrus*** HYDROBIIDAE

The Nautilus, 22:86, pl. 4, figs. 10-11
CM, 104 Syntypes, 62.16336
MZUM, "Types" (ex-Walker coll. 28431)
ANSP, Syntypes, Aldrich, Clapp, Henderson
Type Locality: Coosa River, the Bar, 2½ miles above Yellowleaf
Creek, Chilton Co., Alabama

degener Pilsbry and Hirase, 1904. ***Helicina verecunda*** HELICINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:
625
CM, 4 Syntypes, 62.15655 (ex-Hirase 1255)
ANSP, Syntypes, 87,686 from 1,255 of Hirase
Type Locality: Okinaerabushima, Osumi, Kyushu, Japan

docima Thompson, 1968. ***Heleobops*** HYDROBIIDAE

Hydrobiidae of Florida (University of Florida Press), 23, figs. 48 A-
F; 58 A-B
CM, 51 Paratypes, 65-11 (ex-Thompson)
USNM, Holotype, 636131
MZUM, 200 Paratypes, 216491
MCZ, 35 Paratypes, 258004
ANSP, 30 Paratypes, 301543
Type Locality: Everglades National Park, 9-mile Pond, Dade Co.,
Florida

doellojuradoi Parodiz, 1960. ***Lyrodes*** HYDROBIIDAE

The Nautilus, 74:26, pl. 3, figs. 7-11
CM, Holotype and 93 Paratypes, 43.152 (from MACN)
MZUM, 5 Paratypes (ex-Thompson)
Type Locality: Rio Gualaguaychú, at Gualaguaychú City, Entre Rios,
Argentina

dohertyi Aldrich, 1898. ***Omphalotropis (Selenomphala)*** ASSIMINEIDAE

The Nautilus, 12:3, pl. 1, figs. 1, 2
CM, 1 Syntype, 46774 (ex-Aldrich)
CM, 3 Syntypes, 62.38663 (ex-Clapp from Aldrich)
Type Locality: Marang, Sumatra (indicated on first page of paper)

dohertyi Godwin-Austen, 1892. ***Diplommatina*** CYCLOPHORIDAE

Proceedings of the Zoological Society, London, 513
CM, 2 Syntypes, 46768 (ex-Doherty and ex-Aldrich)
Type Locality: Margarita, Upper Assam, India

domuncula Godwin-Austen, 1892. ***Diplommatina*** CYCLOPHORIDAE

Proceedings of the Zoological Society, London, 518
CM, 1 Syntype, 46769 (ex-Doherty and ex-Aldrich)
Type Locality: Margarita, Naga Hills, India

egerdirensis Weber, 1926. ***Valvata piscinalis*** VALVATIDAE

Reference unknown.

- CM, 25 presumed Syntypes, 62.19857 (ex-Modell from Pfeiffer, collected 1926)
 Type Locality: south of Lake Egerdir, Anatolia, Asia Minor (Turkey)
- engbergi* Bartsch, 1920. *Odostomia (Amaura)* PYRAMIDELLIDAE
 Journal of the Washington Academy of Science, 10:570–571
 CM, 4 Syntypes, 62.38679 (ex-Engberg)
 USNM, Syntypes
 Type Locality: Olga, San Juan Co., Washington
- engbergi* Bartsch, 1920. *Turbonilla (Chemnitzia)* PYRAMIDELLIDAE
 Journal of the Washington Academy of Science, 10:570
 CM, 9 Syntypes, 62.38680 (ex-Engberg)
 USNM, Syntypes
 Type Locality: Friday Harbor, San Juan Co., Washington
- expolita* Pilsbry, 1903. *Helicina reinii* HELICINIDAE
 The Nautilus, 16:131
 CM, 5 Syntypes, 62.15654 (ex-Hirase 55)
 Type Locality: Sezan, Awaji, Honshu, Japan
- flexuosa* Smith, 1922. *Anculosa* PLEUROCERIDAE
 In Goodrich, Miscellaneous Publication, Museum of Zoology, University of Michigan, 7:33, pl. 1, fig. 7; pl. 3, figs. 17–18
 CM, 2 Paratypes, 62.17475 (ex-Clapp from Smith)
 MZUM, Holotype
 ALA, Paratypes
 Type Locality: Coosa River, Wetumpka, Elmore Co., Alabama (coll. Smith, 1904)
- floridanus* Rehder, 1943. *Microdochus* RISSOIDAE
 Proceedings of the United States National Museum, 83:187–203, pl. 20, fig. 6
 = *Cingula (Microdochus) floridanus* (Rehder)
 CM, 8 Paratypes, 62.40550 (ex-Bales)
 USNM, Holotype, 536048
 Type Locality: Missouri Key, Florida Keys (description says: Bonefish Key)
- formicacorsii* Klappenbach, 1962. *Olivella (Orbignytesta)* OLIVIDAE
 Archiv für Molluskenkunde, 91:95, figs. 1–6
 CM, 45 Paratypes, 64,198 (ex-Duarte)
 MNHN, Holotype, 0721; Paratypes, 0722
 Museum Senckenberg, Frankfurt, Paratypes 164986
 Type Locality: La Coronilla, Rocha, Uruguay
- fultoni* Aldrich, 1898. *Leptopoma* CYCLOPHORIDAE
 The Nautilus, 12:3, pl. I, figs. 11, 12
 ?= *Leptopoma matildae* Dohrn
 CM, 1 Syntype, 46765 (ex-Doherty)
 ANSP, Syntypes
 Type Locality: Marang, Sumatra
- funatoi* Pilsbry, 1901. *Pupinella* CYCLOPHORIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:497

CM, 6 Syntypes, 62.15731 (ex-Hirase)
Type Locality: Tane-ga-shima (Hirase 665a)

garrettiana Hartman, 1890. *Orobophana* HELICINIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 42:
287, pl. 3, fig. 11

CM, 4 Syntypes, 62.39824 (ex-Hartman)
Type Locality: Tu-Apu, Marquesas Islands

gibbera Pilsbry and Hirase, 1904. *Diplommatina* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:620
CM, 6 Syntypes, 62.15477 (ex-Hirase)
ANSP, Syntypes, 87,643 from Hirase's 1,027
Type Locality: Nomimura, Tosa, Shikoku, Japan

goodrichi Archer, 1933. *Viviparus contectoides* VIVIPARIDAE
The Nautilus, 47:19, pl. 3, figs. 1-3
= *Viviparus georgianus* (Lea, 1834), *fide* Clench and Fuller, 1965
CM, 3 Paratypes, 46770 (ex-MCZ) and 3 Paratypes, 62.26802
MCZ, Holotype, 92432
Type Locality: Spring-fed stream, tributary of Chipola River, 5 miles
east of Mariana, Jackson Co., Florida

goodrichi Hinkley, 1920. *Goniobasis* PLEUROCERIDAE
Occasional Papers, Museum of Zoology, University of Michigan,
78:1, fig. on p. 3
CM, 3 Paratypes, 62.8127 (ex-Hinkley)
USNM, Paratypes
ANSP, Paratypes
Type Locality: A tributary of Swan Creek Branch, 4 miles east of
Aetna, Hickman Co., Tenn. (coll. Hinkley, 1907)

goviensis Geyer, 1907. *Vitrella suevica* form HYDROBIIDAE
Jahreshefte des Vereins für Vaterländische Naturkunde in Württem-
berg, 1907:411
= *Bythiospeum acicula clessini* form *goviensis* (Geyer)
CM, 2 Paratypes, 62.16777 (ex-Blume)
SMF, Lectotype, Paratypes
Type Locality: Reusten bei Herrenberg, near Tübingen, Württem-
berg, Germany

grenadensis Smith, 1895. *Helicina* HELICINIDAE
Proceedings of the Malacological Society of London, 1:318, pl. 20,
figs. 16-18
CM, 10 Syntypes, 62.2986 (ex-Smith coll.)
BMNH, Syntypes
Type Locality: Cocoa Orchards, Windward, Grenada, West Indies,
under rubbish and rotting leaves, damp places below 500 feet

hachijoensis Pilsbry, 1904. *Euchelus* TROCHIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 65:35
CM, 2 Syntypes, 62.9880
ANSP, Syntype, 85978
Type Locality: Hachijo, Idzu (=Izu, Shizuoka Prefecture), Honshu,
Japan

- hakodadiensis*** Hartman, 1890. *Helicina* HELICINIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 42:
286, pl. 3, fig. 8
CM, 3 Syntypes, 62.15642 (ex-Hartman)
Type Locality: Hakodadi, Japan
- hannibali*** Weaver and Palmer, 1922. *Goniobasis* PLEUROCERIDAE
University of Washington Publications in Geology, 1(3):44–45
CM, 2 “Topotypes,” 62.29912 (ex-Eyerdam). Fossil
Type Locality: near Voder, Washington. Eocene
- harimensis*** Pilsbry, 1900. *Alycaeus* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 52:381
CM, 4 Syntypes, 62.15420 (ex-Hirase)
Type of Locality: Nomimura, Tosa, Shikoku, Japan
- hartmani*** MacMillan, 1946. *Helicina* HELICINIDAE
The Nautilus, 60:33
Replacement name for *H. dominicensis* Hartman, 1890 (not *H. dominicensis* Pfeiffer, 1851), Proceedings of the Academy of Natural Sciences, Philadelphia, 42:286, pl. 3, fig. 9
CM, 9 Syntypes, 62.39823 (ex-Hartman)
Type Locality: Dominique Islands, Marquesas Islands
- hendersoni*** Torre, 1909. *Chondropoma* CHONDROPOMIDAE
The Nautilus, 23:49–50, pl. 4, fig. 6
=*Hendersonina* (*Hendersonina*) *hendersoni* (Torre), NEW COMBINATION
CM, 6 Paratypes, 62.29735 (ex-Jaume)
USNM, Holotype, 492714 (so indicated in label although Torre did not select a type)
Type Locality: Sierra del Ancon, northwest of Viñales, Prov. Pinar del Rio, Cuba
- hendersoni*** Walker, 1909. *Somatogyrys* HYDROBIIDAE
The Nautilus, 22:87, pl. 6, fig. 2
CM, 5 Syntypes, 62.16342
MZUM, “Types” (ex-Walker, 28432)
ANSP, Syntypes, Aldrich, Clapp, Henderson
Type Locality: Duncan’s Riffle, Coosa River, Chilton Co., Alabama
- hinkleyi*** Pilsbry, 1896. *Pomatiopsis* TRUNCATELLIDAE
The Nautilus, 10:37
CM, 6 Syntypes, 62.2554 (ex-Walker and ex-Sterki)
CM, 14 “Topotypes,” 46771 (ex-Walker)
ANSP, Syntypes, 68449
Type Locality: Black Falls, above Florence, Alabama
- hinkleyi*** Walker, 1919. *Amnicola* HYDROBIIDAE
Occasional Papers, Museum of Zoology, University of Michigan, 73:4, pl. 1, fig. 6
CM, 103 Syntypes, 62.16424 (ex-Hinkley)
MZUM, Syntype (ex-Walker coll. 47162)
Type Locality: Reservoir, 4 miles north of Guatemala City, Guatemala

- hirasei* Pilsbry, 1900. *Alycaeus* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 52:382
CM, 6 Syntypes, 62.15426 (ex-Hirase)
Type Locality: Kyoto, Yamashiro (Kyoto Prefecture), Honshu, Japan
- hirasei* Pilsbry, 1901. *Cyclophorus* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53:348
CM, 4 Syntypes, 62.15455 (ex-Hirase)
Type Locality: Oshima [Subprefecture], Hokkaido, Japan (Hirase, 644)
- hirasei* Pilsbry, 1901. *Cyclotus* CYCLOPHORIDAE
The Nautilus, 15:22
CM, 12 Syntypes, 62.15462 (ex-Hirase 612)
Type Locality: "Loo Choo Island" (=Ryukyu Islands, Okinawa Prefecture), Japan (Hirase 612)
- hondurana* Richards, 1938. *Helicina* HELICINIDAE
Proceedings of the American Philosophical Society, 79:174
CM, 2 Paratypes, 62.33059 (ex-Richards)
ANSP, Holotype
Type Locality: Roatan, Honduras
- hyalina* Hartman, 1890. *Helicina* HELICINIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 42: 285, pl. 3, fig. 6
=*Sulfurina parva hyalina* (Hartman, 1890)
CM, 3 Syntypes, 46760 (ex-Hartman coll.)
Type Locality: Mt. Halcone, Mindoro, Philippine Islands
- hypohyalina* Thompson, 1968. *Aphaostracon* HYDROBIIDAE
Hydrobiidae of Florida (University of Florida Press), 80, figs. 62 C-D; figs. 52 D-F
CM, 38 Paratypes, 65-15
MZUM, Holotype, 216527 and 75 Paratypes, 216528; 60 Paratypes, 216529
MCZ, 30 Paratypes, 258009
ANSP, 30 Paratypes, 301541
USNM, 50 Paratypes, 636941
UF, 30 Paratypes
Type Locality: Mill Spring, Ichatucknee Springs, Columbia Co., Florida
- iota* Pilsbry and Hirase, 1904. *Cyathopoma* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:619
CM, 6 Syntypes, 62.15451 (ex-Hirase)
ANSP, Syntypes, 87,698, from Hirase's 1,292
Type Locality: Kumejima, Ryukyu Islands, (Okinawa Prefecture), Japan
- immersidens* Pilsbry and Hirase, 1904. *Diplommatina* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:623
CM, 6 Syntypes, 62.15482 (ex-Hirase)
ANSP, Syntypes, 87,655, from Hirase's 1,299

Type Locality: Miyakojima, Ryukyu Islands, Okinawa Prefecture, Japan

insularum Pilsbry, 1901. *Diplommatina* CYCLOPHORIDAE

The Nautilus, 15:22

CM, 12 Syntypes, 62.15619 (ex-Hirase 620)

Type Locality: Yaeyama, "Loo Choo Islands" (=Ryukyu Islands, Okinawa Prefecture), Japan (Hirase 620)

japonicus Pilsbry, 1901. *Omphalotropis* ASSIMINEIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:405

CM, 16 Syntypes, 62.15712 (ex-Hirase 588)

ANSP, Syntypes, 80966

Type Locality: Kashiwashima, Tosa, Shikoku, Japan, from Hirase, 588

jaumei Torre. *Eutrochatella* HELICINIDAE

Reference and year of publication unknown.

CM, 4 presumed Paratypes, 62.26789 (ex-Jaume)

Type Locality: La Esperanza, Consolacion del Norte, Pinar del Rio, Cuba. Holotype probably at University of Havana.

jayae Parodiz, 1977. *Calliostoma (Tropidotrochus)* TROCHIDAE

Annals of Carnegie Museum, 46:101, Article 8

CM, Holotype (fossil), 43647 (ex-Tripp)

Type Locality: Rice's Pit, Hampton, Virginia in deposits of Upper Yorktown Formation, late Miocene

judii Pilsbry and Cooke, 1908. *Helicina* HELICINIDAE

Occasional Papers, Bernice P. Bishop Museum, 3:208, text fig.

=*Orobophana judii* (Pilsbry and Cooke)

CM, 5 "Topotypes" (fossil), 62.39809 (ex-BPBM 35828)

Type Locality: Kaloa Beach, Kauai, Hawaii

kikaiensis Pilsbry, 1902. *Cyclophorus* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54:27

CM, 6 Syntypes, 62.15456 (ex-Hirase)

ANSP, Syntypes, 81,940 from Hirase's 547

Type Locality: Kikai-ga-shima, Osumi, Kyushu, Japan

kumejimana Pilsbry and Hirase, 1904. *Diplommatina* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:623

CM, 6 Syntypes, 62.15481 (ex-Hirase 1288a)

ANSP, Syntypes, 87,654, from Hirase's 1288a

Type Locality: Kumejima, Ryukyu Islands, Okinawa Prefecture, Japan

labiata Geyer, 1908. *Vitrella* HYDROBIIDAE

Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1904:320

=*Bythiospeum sandbergeri labiatum* (Geyer)

CM, 2 Paratypes, 62.16769 (ex-Blume)

SMF, Lectotype, Paratypes

Type Locality: Wilhelmstal bei Degenfeld, Württemberg, Germany

- laevicervix* Pilsbry and Hirase, 1904. *Alycaeus* CYCLOPHORIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 56:618
 CM, 3 Syntypes, 62.15429 (ex-Hirase)
 ANSP, Syntypes, 87,699 from Hirase's 1,280
 Type Locality: Kuchinaerabushima, Osumi, Kyushu, Japan
- layardi* Hartman, 1888. *Helicina* HELICINIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 40:
 251, pl. 13, figs. 6, 6a
 =*Pleuropoma sublaevigata* (Pfeiffer), *fide* Solem, 1959
 CM, Lectotype and 2 Paralectotypes, 62.15656
 Type Locality: Aura Islands, New Hebrides
- luchuana* Pilsbry, 1901. *Eulima* MELANELLIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:
 396, pl. 21, fig. 29
 =*Melanella luchuana* (Pilsbry)
 CM, 6 Syntypes, 62.9898 (ex-Hirase)
 ANSP, Syntypes, 80,628, from Hirase 1,275
 Type Locality: "Loo Choo Islands" (=Ryukyu Islands, Okinawa Prefecture), Japan
- magdalenae* Ancey, 1890. *Orobophana* HELICINIDAE
 Bulletin de Société Malacologique de France, 7:342
 =*Orobophana constricta* (Pfeiffer)
 CM, 3 "Topotypes," 62.39811 (ex-BPBM 16140)
 Type Locality: Mt. Tantalus, Oahu, Hawaii
- major violacea* Monterosato, 1877. *Clathurella linearis* var. TURRIDAE
 Nuova Rivista delle Conchiglie Mediterranee, Atti Acc. Palermo,
 44 (see Manual of Conchology, 6(1884):277), not [*C. violacea*
 Pease = *C. clandestina* Deshayes]
 =*Pleurotomoides concinna* Scacchi
 CM, 1 Syntype, 62.17269 (ex-Blume)
 Type Locality: Palermo, Sicily, Italy
- medinae* Parodiz, 1955. *Triphora* TRIPHORIDAE
 Neotropica, 1:59, 1 figure
 CM, Holotype and 18 Paratypes, 43077 (ex-de Medina)
 ANSP, 1 Paratype
 Type Locality: Playa de Punta Carretas, Montevideo, Uruguay
- melanioides* von Martens, 1899. *Amnicola*? HYDROBIIDAE
 Biologia Centrali Americana, 436, pl. 22, fig. 8
 CM, 7 "Topotypes," 62.16424 (ex-Biolley, "N. H. Costa Rica Mus.")
 Natural History Museum, Neufchâtel, France, Syntypes
 Type Locality: Rio Plantanales, Golfo Dulce, W. Costa Rica
- meyense* Torre and Bartsch, 1938. *Chondropoma* (*Chondropomorus*) *aubermanum*
 CHONDROPOMIDAE
 Proceedings of the United States National Museum, 85:375, pl. 34,
 fig. 2
 CM, 6 Paratypes, 62.26795 (ex-Jaume)
 USNM, Holotype, 134930

Type Locality: Palma Sola east of Punta de Maya, between Matanzas and Cardenas, Cuba

miamiensis Pilsbry, 1899. *Ampullaria* AMPULLARIIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 51:365
=*Pomacea miamiensis* (Pilsbry)

CM, 1 Paralectotype, 62.19966 (ex-Clapp)

CM, 1 Paralectotype (juvenile), 62.33743 (ex-Clapp)

ANSP, Lectotype, 77369 (H. B. Baker, 1964)

Type Locality: in a creek flowing from the Everglades, near Miami, Dade Co., southeast Florida

mica Thompson, 1968. *Cincinnatia* HYDROBIIDAE

Hydrobiidae of Florida (University of Florida Press), 127, fig. 66E
CM, 84 Paratypes, 65-8

MZUM, Holotype, 216494, and 200 Paratypes, 216495

USNM, 30 Paratypes, 636939

ANSP, 30 Paratypes, 301538

MCZ, 35 Paratypes, 258012

Type Locality: Small spring west bank of Ichetucknee River, 1 mile N. E. Highway 27, Suwannee Co., Florida

micra Pilsbry and Ferris, 1906. *Valvata* HYDROBIIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 58:
172, pl. 9, figs. 7-9

=*Horatia micra* (Pilsbry and Ferris)

CM, 14 Syntypes, 62.20173 (ex-Pilsbry)

ANSP, Holotype, 91322 (type indicated on plate)

Type Locality: Drift, Guadalupe River, 4 miles above New Braunfels, Comal Co., Texas

micron Pilsbry, 1900. *Cyclotus?* CYCLOPHORIDAE

The Nautilus, 14:12

=*Cyanthopoma micron* (Pilsbry, 1900)

CM, 10 Syntypes, 62.15452 (ex-Hirase 307)

Type Locality: Kashima, Harima (Hyogo Prefecture), Honshu, Japan

microtheca Pilsbry, 1902. *Helicina yoshiwarana* HELICINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54:
26. Figured in Wagner 1905, t. 5, fig. 4

=*Aphanocomia yoshiwarana microtheca* (Pilsbry)

CM, 6 Syntypes, 62.15649 (ex-Hirase 857)

Type Locality: Ogasawara-jima, Bonin Islands, Japan

misionum Parodiz, 1966. *Potamolithus peristomatus* HYDROBIIDAE

The Nautilus, 80:57, pl. 4, figs. 1-4

CM, Holotype and 10 Paratypes, 59-113 (ex-Parodiz, 1959)

Type Locality: San Javier, on the Uruguay River, Misiones, N. W. Argentina

modestus A. Adams, 1850. *Cerithium* CERITHIIDAE

Contributions to Conchology, 7:117. Illustrated in Clench and Turner, 1950, Occasional Papers, Museum of Comparative Zoology, pl. 39, fig. 8

=*Triphora modesta* (A. Adams)

CM, 2 Syntypes, 62.3774 (ex-Holland)

Type Locality: Jamaica

monardi Haas, 1934. *Viviparus*

VIVIPARIDAE

Zoologische Anzeiger, Leipzig, 106:237, pl. 1-6

=*Bellamya monardi* (Haas)

CM, Holotype and 1 Paratype, 62.32347 (ex-Rudyard Boulton)

Type Locality: Cumene River, Mulondo, Angola, Africa

moriciandi Möllendorff. *Cyclophorus*

CYCLOPHORIDAE

Reference and year of publication unknown.

Not *C. moriciandi* (Pfeiffer, 1852)

CM, 1 presumed Paratype, 62.29512 (ex-Eyerdam from Möllendorff)

Type Locality: Hubei, Philippine Islands

muskusi H. B. Baker, 1924. *Tudora*

CHONDROPOMIDAE

The Nautilus, 37:93

=*Licina muskusi* (H. B. Baker)

CM, 21 Paratypes, 62.26816

MZUM, Holotype (?)

Type Locality: Top of shore cliffs, Knip Baai, Northern Curacao, Dutch Leeward Islands

nakadai Pilsbry, 1901. *Spiropoma*

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:496

=*Spiristoma nakadai* (Pilsbry)

CM, 6 Syntypes, 62.15747 (ex-Hirase)

Type Locality: Tane-ga-shima (Hirase 658)

nelsoni Clapp, 1914. *Colobostylus*

CHONDROPOMIDAE

The Nautilus, 27:99

=*Licina nelsoni* (Clapp), NEW COMBINATION

CM, 2 Syntypes, 46773 (ex-Nelson)

MCZ, Syntypes, 22879

Type Locality: Swan Island, Caribbean Sea

nigrocinctus C. B. Adams, 1839. *Cerithium*

CERITHIDAE

Boston Journal of Natural History, 2:286, pl. 4, fig. 11

=*Triphora nigrocincta* (C. B. Adams)

CM, 1 Syntype, 62.3773 (ex-Holland) Cabinet, Boston Society of Natural History, Syntype (now in MCZ)

Type Locality: Massachusetts

nounouensis Neal, 1934. *Pleuropoma*

HELICINIDAE

Hawaiian Helicinidae, Bulletin of the Bernice P. Bishop Museum, 125:79, figs. 92-94

CM, 3 Paratypes, 62.39803 (ex-BPBM 81121)

BPBM, Holotype, 11213

Type Locality: Nounou Mts., Kauai, northeast side, Hawaii

obteca Möllendorff. *Cyclophorus philippinarum*

CYCLOPHORIDAE

Reference unknown.

CM, 2 presumed Paratypes, 62.29513 (ex-Eyerdam from Möllendorff)

Type Locality: Illocos, Philippine Islands

ogasawarana Pilsbry, 1902. *Helicina* HELICINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54: 25. Figured in Wagner 1905, t. 5, fig. 5

=*Aphanocomia ogasawarana* (Pilsbry)

CM, 3 Syntypes, 62.15646 (ex-Hirase 808)

Type Locality: Ogasawara-jima, Bonin Islands, Japan

ogasawarana Pilsbry, 1905. *Planaxis abbreviatus* PLANAXIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 57: 105, pl. 3, figs. 18–19

CM, 6 Syntypes, 62.9908 (ex-Hirase 1629)

Type Locality: Hahojima, Bonin Islands, Ogasawara, Japan

ogasawarana Pilsbry, 1904. *Rissoa* RISSOIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56: 26, pl. 4, fig. 41

=*Rissoia ogasawarana* (Pilsbry)

CM, 12 Syntypes, 62.9916 (ex-Hirase 1385)

ANSP, Syntypes, 85,951, from 1,385 of Hirase

Type Locality: Hahajima, Ogasawara, Japan

omiensis Pilsbry, 1900. *Diplommatina pusilla* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 52:382

CM, 10 Syntypes, 62.15465 (ex-Hirase)

ANSP, Syntypes, 49452a

Type Locality: Ibuki, Prov. Omi (Shiga Prefecture), Honshu, Japan

onoensis Pilsbry and Hirase, 1904. *Diplommatina goniobasis* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:621

CM, 6 Syntypes, 62.15478 (ex-Hirase 1027a)

Type Locality: Onomura, Tosa, Shikoku, Japan

opisthocoelicum Torre. *Rhytidothyroma?* CHONDROPOMIDAE

Reference and year of publication unknown.

CM, 4 presumed Paratypes, 62.27694 (ex-Jaume)

Type Locality: Loma Santa Clara, Calabazar de Sagua, Santa Clara, Cuba

orientalis Neal, 1934. *Pleuropoma (Spaerocomia) kauaiensis* var. HELICINIDAE

Bulletin of the Bernice P. Bishop Museum, 91, fig. 110

CM, 1 "Topotype," 62.39802 (ex-BPBM 81063)

BPBM, Holotype, 11242

Type Locality: Nounou Mts., Kauai, west side, Hawaii

ornata Lea, 1868. *Goniobasis* PLEUROCERIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 20: 152 (in Latin)

CM, 4 "Topotypes," 62.33573 (ex-Goodrich from Clench)

Type Locality: Connesauga Creek, Georgia

- oshimae* Pilsbry, 1901. *Pupinella* CYCLOPHORIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:349
 CM, 6 Syntypes, 62.15729 (ex-Hirase 645)
 ANSP, Syntypes, 81228a
 Type Locality: Oshima, Osumi, Kyushu, Japan
- oshimanus* Pilsbry and Hirase, 1904. *Alycaeus* CYCLOPHORIDAE
 The Nautilus, 18:7
 CM, 6 Syntypes, 62.15433 (ex-Hirase 931)
 ANSP, Syntypes, 83385 (from 931 of Hirase collection)
 Type Locality: Oshima, Osumi, Kyushu, Japan
- osumiensis* Pilsbry, 1901. *Helicina* HELICINIDAE
 The Nautilus, 14:127. Figured in Wagner, 1905, Helicinenstudien,
 t. 4, fig. 9
 =*Aphanocomia osumiensis* (Pilsbry)
 CM, 16 Syntypes, 62.15640 (ex-Hirase 558)
 Type Locality: Kikai, Osumi, Kyushu, Japan
- ozarkensis* Hinkley, 1916. *Pyrgulopsis* HYDROBIIDAE
 Proceedings of the United States National Museum, 49:588, pl. 78,
 fig. 2
 =*Pyrgulopsis ozarki* Hinkley (on label)
 CM, 6 Paratypes, 62.8928 (ex-Hinkley, 1914)
 ALA, 13 Paratypes, 2646
 Type Locality: North Fork White River, Norfolk, Baxter Co., Ar-
 kansas
- pallida* Monterosato, 1875. *Daphnella nebula* var. TURRIDAE
 Nuova Rivista delle Conchiglie Mediterranee, Atti Acc. Palermo,
 1875:1-50.
 =*Raphitoma nebula* form *pallida* (Monterosato)
 CM, 2 Syntypes, 62.17272 (ex-Blume)
 Type Locality: Palermo, Sicily, Italy
- panzogensis* Walker, 1919. *Amnicola* HYDROBIIDAE
 Occasional Papers, Museum of Zoology, University of Michigan,
 73:3, pl. 1, figs. 2-3
 CM, 69 Syntypes, 62.16286 (ex-Hinkley)
 MZUM, "Type" (ex-Walker coll. 37387)
 Type Locality: Panzog, Guatemala
- petrifons* Thompson, 1968. *Cincinnatia* HYDROBIIDAE
 Hydrobiidae of Florida (University of Florida Press), 138, fig. 67D
 CM, 76 Paratypes, 65-7 (ex-Thompson)
 MZUM, Holotype, 216501, and 500 Paratypes, 216502
 USNM, 90 Paratypes, 636936
 ANSP, 30 Paratypes, 301536
 MCZ, 130 Paratypes, 258015
 UF, 100 Paratypes
 Type Locality: Rock Springs, Orange Co., Florida
- pfeifferi* Weber. *Pyrgula* TRUNCATELLIDAE?
 Reference and year of publication unknown.

CM, 2 presumed Syntypes ("Types" on label), plus 3 presumed Paratypes, 62.19859 (ex-Modell from Pfeiffer)

Type Locality: south end Lake Egerdir, Anatolia, Asia Minor, Turkey

photophila Geyer, 1907. *Vitrella* HYDROBIIDAE

Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1907:408

=*Bythiospeum sandbergeri labiatum* (Geyer)

CM, 1 Paratype, 62.16768 (ex-Blume)

SMF, Lectotype

Type Locality: Gruibingen, Württemberg, Germany

ponderosa Thompson, 1968. *Cincinnati* HYDROBIIDAE

Hydrobiidae of Florida (University of Florida Press), 137, fig. 67C

CM, 115 Paratypes, 65-6

MZUM, Holotype, 216499, and 500 Paratypes, 216500

USNM, 120 Paratypes, 636933

MCZ, 140 Paratypes, 258013

ANSP, 30 Paratypes, 301545

UF, 100 Paratypes

Type Locality: Outlet from Sanlando Springs, 3 miles west of Longwood, Seminole Co., Florida

postera Geyer, 1904. *Vitrella franconia* var. HYDROBIIDAE

Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1904:327

=*Bythiospeum acicula clessini* (Weinland)

CM, 1 Paratype, 62.16774 (ex-Blume)

SMF, Lectotype, Paratypes

Type Locality: Maubachquelle bei Backnang, Württemberg, Germany

praelonga Brooks and MacMillan, 1940. *Pomatiopsis* TRUNCATELLIDAE

The Nautilus, 54:96

CM, Holotype, 62.32897 (ex-MacMillan)

CM, 1 Paratype, 62.32898

USNM, Paratypes, 473964

ANSP, Paratypes, 174910

Type Locality: Elk River and Camp Creek valleys, 1.5 miles south of Clay, Clay Co., West Virginia

pudica Pilsbry, 1902. *Diplommatina* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54:28

CM, 6 Syntypes, 62.15475 (ex-Hirase)

ANSP, Syntypes, 82652 from 836a of Hirase

Type Locality: Nachi, Kii [Province], Honshu, Japan

purus Pilsbry and Hirase, 1904. *Alycaeus* CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:617

CM, 6 Syntypes, 62.15430 (ex-Hirase 219)

ANSP, Syntypes, 87683, from Hirase's 219

Type Locality: Tokunoshima, Osumi, Kyushu, Japan

- putei* Geyer, 1904. *Vitrella* HYDROBIIDAE
Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1904:317
= *Bythiospeum sandbergeri putei* (Geyer)
CM, 3 Paratypes, 62.16770 (ex-Blume)
SMF, Lectotype, Paratypes
Type Locality: Treitschachbrunnen bei Kohlberg, Württemberg, Germany
- pygmaeus* Walker, 1909. *Somatogyrus* HYDROBIIDAE
The Nautilus, 22:88, pl. 6, fig. 3
CM, 7 Syntypes, 62.16358 (ex-Smith and Clapp)
MZUM, "Types" (ex-Walker coll. 28433)
ANSP, Syntypes, Aldrich, Clapp, Henderson
Type Locality: Coosa River, The Bar, 2½ miles above Yellowleaf Creek, Chilton Co., Alabama
- quaranitica* Doering, 1885. *Lyrodes* HYDROBIIDAE
Boletín de la Academia Nacional de Ciencias, Córdoba, 7:457-474, figs. a-b
The Nautilus, 74:24, pl. 3, figs. 1-5 (for Neotype)
CM, Neotype and 100 Paraneotypes, 59-108 (ex-Carcelles)
Type Locality: Arroyo Riachuelo, near Corrientes City, Argentina
- quesadai* Aguayo, 1932. *Opisthosiphon* CHONDROPOMIDAE
The Nautilus, 45:95, pl. 6, fig. 5
CM, 6 Paratypes, 62.26796 (ex-Jaume)
Type Locality: La Cantera San German, Holguin, Oriente, Cuba
- reinhardti* Pilsbry, 1900. *Alycaeus* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 52:381
= *Alycaeus pilsbryi* Kobelt
CM, 6 Syntypes, 62.15422 (ex-Hirase)
ANSP, Syntypes, 84768a
Type Locality: Kashima, Harima (Hyogo Prefecture), Honshu, Japan
- rhadinus* Thompson, 1968. *Aphaostracon* HYDROBIIDAE
Hydrobiidae of Florida (University of Florida Press), 78, figs. 52A, C, K; 62 A-B
CM, 62 Paratypes, 65-16 (ex-Thompson)
MZUM, Holotype, 216525, and 200 Paratypes, 216526
USNM, 100 Paratypes, 636944
MCZ, 50 Paratypes, 258008
ANSP, 30 Paratypes, 301546
UF, 50 Paratypes
Type Locality: Fish Creek at Florida Highway 209, 3.3 miles east of U.S. Highway 17, 3.7 miles south of Bostwick, Putnam Co., Florida
- roatanensis* Richards, 1938. *Choanopoma andrerosae* CHONDROPOMIDAE
Proceedings of the American Philosophical Society, 79:174, pl. 3, fig. 1
= *Annularia andrerosae roatanensis* (Richards), NEW COMBINATION

CM, 5 Paratypes, 62.33056 (ex-Richards)
 ANSP, Paratypes, 170018
 Type Locality: West End, Roatan, Honduras

roesleri Geyer, 1904. *Vitrella putei* var. HYDROBIIDAE
 Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1904:318
 = *Bythiospeum sandbergeri putei* (Geyer)
 CM, 1 Paratype, 62.16771 (ex-Blume)
 SMF, Lectotype, Paratypes
 Type Locality: Offerdingen, Württemberg, Germany

rondeklipensis H. B. Baker, 1924. *Tudora megacheilus* CHONDROPOMIDAE
 Occasional Papers, Museum of Zoology, University of Michigan, 152:60
 = *Licina megacheilus rondeklipensis* (H. B. Baker)
 CM, 6 Paratypes, 62.26813 (ex-Goodrich)
 MZUM, Holotype
 Type Locality: Base of northern escarpment, Ronde Klip, Curacao, Dutch Leeward Islands

sadoensis Pilsbry and Hirase, 1903. *Helicina* HELICINIDAE
 The Nautilus, 16:128. Figured in Wagner 1905, pl. 7, fig. 11
 = *Hemipoma sadoensis* (Pilsbry and Hirase)
 CM, 6 Syntypes, 62.15651 (ex-Hirase 991)
 ANSP, Syntypes, 84380, from 991 of Hirase coll.
 Type Locality: Sotokaifu, Sado, Honshu, Japan

sadoensis Pilsbry and Hirase, 1903. *Japonia* CYCLOPHORIDAE
 The Nautilus, 17:31
 CM, 3 Syntypes, 62.15657 (ex-Hirase)
 ANSP, Syntypes, 84768a
 Type Locality: Niibo-mura, Sado, Honshu, Japan

sanctaemarthae Pilsbry and Clapp, 1902. *Aperostoma* CYCLOPHORIDAE
 The Nautilus, 15:134, pl. 7, figs. 9–10
 = *Cyclotus sanctaemarthae* (Pilsbry and Clapp)
 CM, Holotype, 62.15065 (a single specimen collected by Mr. and Mrs. H. H. Smith)
 Type Locality: Las Nubes estate, Santa Marta Mts., Colombia, alt. 4000 feet

sanctaemarthae Pilsbry and Clapp, 1902. *Helicina* HELICINIDAE
 The Nautilus, 15:136, pl. 7, fig. 4
 CM, Holotype and 9 Paratypes, 46762 (ex-Smith)
 Type Locality: Santa Marta Mts., Colombia, at El Libano, 6000 feet

sanjuanensis Bartsch, 1921. *Alvania* RISSOIDAE
 Proceedings of the Biological Association of Washington, 34:37–38
 CM, 10 Paratypes, 62.38676 (ex-Engberg)
 Engberg coll., Holotype (now in USNM)
 Type Locality: False Bay, Friday Harbor, San Juan Co., Washington

sanjuanensis Bartsch, 1920. *Barleeia* RISSOIDAE
 Proceedings of the United States National Museum, 58:170–171, pl. 13, fig. 3

CM, 1 Paratype, 62.38677 (ex-Engberg)

USNM, Holotype, 334488

Type Locality: Friday Harbor, San Juan Co., Washington (Original description says, "Gulf of Georgia")

saxoniana Hartman, 1889. *Helicina*

HELICINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 41: 93, pl. 5, fig. 10

ANSP, Holotype, 60065

CM, Paratype, 46920 (ex-Hartman)

Type Locality: New Caledonia

septentrionalis Pilsbry, 1901. *Diplommatina*

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:352

CM, 2 Syntypes, 62.15470 (ex-Hirase)

ANSP, Syntypes, 81001a

Type Locality: Kayabe, Ojima, Hokkaido, Japan (Hirase 639)

simplex Pilsbry, 1902. *Blanfordia japonica* var.

TRUNCATELLIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 54:26

=*Pomatiopsis simplex* (Pilsbry), *fide* H. B. Baker, 1964

CM, 6 Syntypes, 62.15438 (ex-Hirase 406)

ANSP, "Types," 78,836, from Hirase's 406

Type Locality: Nishigo, Uzen (Yamagata Prefecture), Honshu, Japan

stokesii Neal, 1934. *Orobophana*

HELICINIDAE

Hawaiian Helicinidae, Bulletin of the Bernice P. Bishop Museum, 125:15-16, figs. 6-7

CM, 3 Paratypes, 62.39810 (ex-BPBM 35829)

BPBM, Holotype, 11246

Type Locality: Makahuena Point, Koloa, Kauai, Hawaii

submenkeanus Pilsbry, 1901. *Tritonidea*

BUCCINIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53: 387, pl. 21, fig. 24

=*Cantharus submenkeanus* (Pilsbry)

CM, 6 Syntypes, 62.9946 (ex-Hirase 1027)

ANSP, "Types," 80,538, from Hirase's 1,037

Type Locality: Hirado, Hizen, Kyushu, Japan

subtilis Godwin-Austen, 1892. *Diplommatina*

CYCLOPHORIDAE

Proceedings of the Zoological Society, London, 517

CM, 2 Syntypes, 46767 (ex-Doherty coll. from Aldrich)

Type Locality: Margarita, Assam, India

suevica Geyer, 1905. *Vitrella*

HYDROBIIDAE

Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1905:300

=*Bythiospeum acicula clessini* (Weinland)

CM, 1 Paratype, 62.16772 (ex-Blume)

SMF, Lectotype, Paratypes

Type Locality: Herrenberg, Württemberg, Germany

sulcata Smith, 1922. *Anculosa*

PLEUROCERIDAE

In Goodrich, Miscellaneous Publication, Museum of Zoology, University of Michigan, 7:46, pl. 5, figs. 4-5; pl. 3, fig. 20

CM, 9 Paratypes, 62.17489 (ex-Clapp from Smith)

MZUM, Holotype

ALA, Paratypes

Type Locality: Twin Island Shoals, Coosa River, St. Clair Co., Alabama (coll. Smith, 1914)

superbum Henderson and Simpson, 1903. *Chondropoma*

CHONDROPOMIDAE

The Nautilus, 16:88

CM, 6 Syntypes, 62.38661 (ex-Henderson)

Type Locality: On high limestone hill back of Thomazeau, Haiti

tanegashimae Pilsbry, 1901. *Diplommatina*

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:497

CM, 10 Syntypes, 62.15471 (ex-Hirase 668)

ANSP, Syntypes, 82662a

Type Locality: Tane-ga-shima, Japan (Hirase 668)

tanegashimae Pilsbry, 1901. *Pupinella rufa* var.

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:497

=small form of *Pupinella rufa*

CM, 6 Paralectotypes, 62.15730 (ex-Hirase)

ANSP, Lectotype, 81571a, selected by H. B. Baker, 1964

Type Locality: Tane-ga-shima, "Loo Choo Islands" (=Ryukyu Islands, Okinawa Prefecture), Japan

tartarea Hubricht, 1962. *Fontigens*

HYDROBIIDAE

The Nautilus, 76:140, pl. 8, figs. C-D

CM, 15 Paratypes, 46775 (ex-Leslie Hubricht A4845)

FMNH, Holotype, 116917

Type Locality: Stream in Organ Cave, near Organ Cave Post Office, Green Briar Co., West Virginia

tenuis Geyer, 1905. *Vitrella saxigena* var.

HYDROBIIDAE

Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg, 1905:297

=*Bythiospeum quenstedti saxigenum* (Geyer)

CM, 2 Paratypes, 62.16767 (ex-Blume)

SMF, Lectotype, Paratype

Type Locality: Mulheim, Württemberg, Germany

theiocrentus Thompson, 1968. *Aphaostrakon*

HYDROBIIDAE

Hydrobiidae of Florida (University of Florida Press), 87, figs. 53G, I, K; 63E, F

CM, 90 Paratypes, 65-14 (ex-Thompson)

MZUM, Holotype, 216510, and 350 Paratypes, 216511

USNM, 100 Paratypes, 636940

MCZ, 85 Paratypes, 258011

ANSP, 30 Paratypes, 301544

UF, 30 Paratypes

Type Locality: Clifton Springs Run, 2 miles north Oviedom, Seminole Co., Florida

tokunishimana Pilsbry and Hirase, 1904. *Diplommatina*

CYCLOPHORIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 56:622

CM, 6 Syntypes, 62.15480 (ex-Hirase 1217)
ANSP, Syntypes, 87,649 from Hirase's 1,217
Type Locality: Tokunoshima, Osumi, Kyushu, Japan

tokunoshimana Pilsbry and Hirase, 1904. *Japonia* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:616
CM, 4 Syntypes, 62.15659
ANSP, Syntypes, 87,512 from Hirase's 1,206
Type Locality: Tokunoshima, Osumi, Kyushu, Japan

tokunoshimana Pilsbry and Hirase, 1904. *Pupinella oshimae* var. CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:618
CM, 6 Syntypes, 62.15732 (ex-Hirase)
ANSP, Syntypes, 87,506 from Hirase's 1,214
Type Locality: Tokunoshima, Osumi, Kyushu, Japan

tokunoshimanus Pilsbry and Hirase, 1904. *Alycaeus* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:617
CM, 6 Syntypes, 62.15431 (ex-Hirase)
ANSP, Syntypes, 87,505 from Hirase's 931a
Type Locality: Tokunoshima, Osumi, Kyushu, Japan

tosana Pilsbry and Hirase, 1904. *Diplommata* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 56:620
CM, 6 Syntypes, 62.15476 (ex-Hirase)
ANSP, Syntypes, 84,190 from Hirase's 1,026
Type Locality: Nogawa, Tosa, Shikoku, Japan

tristis Pilsbry, 1903. *Phasianella* PHASIANELLIDAE
The Nautilus, 17:69
CM, 6 Syntypes, 62.9875 (ex-Hirase 1367)
ANSP, Syntypes, 85222 from Hirase's 1367
Type Locality: Rishiri, Kitami, Hokkaido, Japan

truncata Vanatta, 1924. *Paludestrina* HYDROBIIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 76:
26-27, text figs. 5-7
= "*Hydrobia*" *truncata* (Vanatta)
CM, 10 "Topotypes," 62.33137 (ex-Bales from Jackson)
ANSP, Lectotype (H. B. Baker, 1964), 132886 (collected by Jackson)
Type Locality: Town Point, Little Choptank River, Maryland

tryoni Lewis, 1871. *Anculosa* PLEUROCERIDAE
American Journal of Conchology, 6:221 (figure not indicated by the
author in text, but corresponds to pl. 17, fig. 8)
CM, 17 "Topotypes," 62.8920 (ex-Ortmann)
Type Locality: Tennessee River, Concord, Knox Co., Tennessee

turris Pilsbry, 1901. *Diplommata* CYCLOPHORIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53:350
CM, 6 Syntypes, 62.15466 (ex-Hirase 648)
ANSP, Syntypes, 81229a
Type Locality: Oshima [Subprefecture], Hokkaido, Japan (Hirase 648)

- unciale*** Haldeman, 1841. *Melania* PLEUROCERIDAE
Monograph of the Limneidae (Dorsey Print., Philadelphia), Part
4, p. 3 of cover, 10/5/1841
=*Pleurocera unciale* (Haldeman)
CM, 8 "Topotypes," 62.33534 (ex-Goodrich)
Type Locality: Beaver Creek, Bristol, Virginia (original description
says "N. E. Tennessee")
- undosa*** Anthony, 1854. *Melania* PLEUROCERIDAE
Annals of the New York Lyceum of Natural History, 6:124, pl. 3,
fig. 25
=*Goniobasis undosa* (Anthony)
CM, 29 Paratypes, 46776 (ex-MCZ)
MCZ, Holotype (?)
Type Locality: Nolin River, Kentucky
- usenensis*** Pilsbry and Gulick, 1900. *Diplommata* CYCLOPHORIDAE
The Nautilus, 14:88
CM, 12 Syntypes, 62.15618 (ex-Hirase 510)
ANSP, Syntypes, 510 of Hirase
Type Locality: Nishigo, Uzen (Yamagata Prefecture), Honshu, Japan
- uzenensis*** Pilsbry, 1901. *Helicina reinii* var. HELICINIDAE
The Nautilus, 14:128
=*Helicina japonica uzensis* (Pilsbry)
CM, 12 Syntypes, 62.15652 (ex-Hirase 575)
Type Locality: Hishigo, Uzen (Yamagata Prefecture), Honshu, Japan
- vallesensis*** Hinkley, 1907. *Pachychilus* PLEUROCERIDAE
The Nautilus, 21, 1907, 25, pl. 5, figs. 1–10
CM, 14 Paralectotypes, 62.7962 (ex-Hinkley)
ANSP, Lectotype (specimen figure #1; subsequent designation by
H. B. Baker, 1964)
Type Locality: Valles River, Valles, San Luis Potosi, Mexico
- varicifera*** Pilsbry, 1901. *Turbonilla* PYRAMIDELLIDAE
Proceedings of the Academy of Natural Sciences, Philadelphia, 53:198
CM, 3 Paratypes, 62.9901 (ex-Hirase 1238)
ANSP, "Types"
Type Locality: Hirado, Hizen, Kyushu, Japan
- viana*** Morelet, 1849. *Helicina* HELICINIDAE
Testacea Novissima Insulae Cubanae, 1:19
=*Viana regina* (Morelet)
CM, 5 "Topotypes," 62.28903
Type Locality: Guajaibon, Pinar del Rio, Cuba
- vianai*** Parodiz, 1960. *Littoridina* HYDROBIIDAE
Neotropica, 6(21):89, figs. a, b
CM, Holotype and 19 Paratypes, 59–107 (coll. Viana, 1959)
Type Locality: Guayapa Patquia (in small lake of salty water), La
Rioja, Argentina
- violacea*** Monterosato, 1877. *Clathurella linearis* var. *major* TURRIDAE
See *major violacea* Monterosato, 1877

- walkeri* Goodrich, 1928. *Strephobasis* PLEUROCERIDAE
Occasional Papers, Museum of Zoology, University of Michigan,
192:14
=*Pleurocera walkeri* (Goodrich)
CM, 5 Paratypes, 62.18518 (ex-Goodrich)
MZUM, Holotype
Type Locality: Sequatchie River, Jasper, Marion Co., Tennessee
- walkeri* Pilsbry and Johnson, 1912. *Viviparus* VIVIPARIDAE
The Nautilus, 26:48, pl. 3, figs. 6-7
=*Viviparus georgianus* (Lea)
CM, 6 Paralectotypes, 62.12706 (ex-Pilsbry)
ANSP, Lectotype, 70,053 (subsequent designation by H. B. Baker,
1964)
Type Locality: Juniper Creek, west side of Lake George, Lake Co.,
Florida
- walkeri* Smith, 1922. *Gyrotoma* PLEUROCERIDAE
In Goodrich, Miscellaneous Publication, Museum of Zoology, Uni-
versity of Michigan, 12:25, pl. 2, figs. 30-32
CM, 6 Paratypes, 62.18944 (ex-Clapp from Smith)
ALA, Paratypes
MZUM, Holotype
Type Locality: Cedar Island, Coosa River, Chilton Co., Alabama
- wassauensis* H. B. Baker, 1924. *Tudora aurantia* CHONDROPOMIDAE
Occasional Papers, Museum of Zoology, University of Michigan,
152:48
=*Licina aurantia wassauensis* (H. B. Baker), NEW COMBINATION
CM, 21 Paratypes, 62.26817 (ex-Goodrich)
MZUM, Holotype
Type Locality: Seroe Wassau, west of entrance to the Goto, Bonaire,
Dutch Leeward Islands
- weinlandi* Geyer, 1904. *Vitrella quenstedti* var. HYDROBIIDAE
Jahreshefte des Vereins für Vaterländische Naturkunde in Württem-
berg, 1904:316
=*Bythiospeum quenstedti* (Wiedersheim)
CM, 2 Paratypes, 62.16766 (ex-Blume)
SMF, Lectotype, Paratypes
Type Locality: Urach, Württemberg, Germany
- westpuntensis* H. B. Baker, 1924. *Tudora fossor* CHONDROPOMIDAE
Occasional Papers, Museum of Zoology, University of Michigan,
152:66
=*Licina fossor westpuntensis* (H. B. Baker), NEW COMBINATION
CM, 5 PARATYPES, 62.26815 (ex-Goodrich coll.)
MZUM, Holotype
Type Locality: Small limestone remnant, near Plaja Abau, Curacao,
Dutch Leeward Islands
- windhausenii* Parodiz, 1961. *Valvata* VALVATIDAE
The Nautilus, 75(1): pl. 1, figs. 3-6
=*Potamolithus windhausenii* (Parodiz)

CM, Holotype, 59–106a (ex-Wichmann, 1928)

CM, 4 Paratypes, 59–106 (ex-Wichmann)

Type Locality: Jahuel Formation (Paleocene), Nahuel Niyeu, 25 miles west of Valcheta, Prov. Rio Negro, Argentina

- yaeyamensis* Pilsbry, 1901. *Helicina* HELICINIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 53:497
 CM, 10 Syntypes, 62.15644 (ex-Hirase 624)
 ANSP, Syntypes, 80,967
 Type Locality: Yaeyama (Okinawa), in southwestern group of the “Loo Choo Islands” (=Ryukyu Islands, Okinawa Prefecture), Japan (Hirase, 624)

- yakushimae* Pilsbry, 1901. *Diplommatina* CYCLOPHORIDAE
 The Nautilus, 15:64
 CM, 6 Syntypes, 62.15621 (ex-Hirase 679)
 ANSP, Syntypes, 81998a
 Type Locality: Yakushima, Osumi, Kyushu, Japan (Hirase, 679)

Gastropoda

Opisthobranchia

- attenuata* Cooke, 1911. *Leptachatina* AMASTRIDAE
 in Pilsbry's Manual of Conchology, (2):69, pl. 7, figs. 45–46
 CM, 2 Paratypes, 62.39816 (ex-Cooke, ex-BPBM 14592)
 BPBM, Holotype, 14592
 Type Locality: Haleieie, Kauai, Hawaii

- borealis* Pilsbry and Hirase, 1904. *Carychium pessimum* var. ELLOBIIDAE
 The Nautilus, 17:119
 CM, 6 Syntypes, 62.15442 (ex-Hirase 1144)
 ANSP, “Types,” 85772, from Hirase's 1144
 Type Locality: Harutori, Hokkaido, Japan

- canadense* Clapp, 1906. *Carychium exile* form ELLOBIIDAE
 The Nautilus, 19:139, pl. 8, figs. 1, 2, 6, 7
 CM, 10 Syntypes and orig. lot, 46537
 Type Locality: Kennebunkport, Maine

- cynatoplax* Pilsbry, 1901. *Carychium* ELLOBIIDAE
 The Nautilus, 15:23
 CM, 10 Syntypes, 62.15439 (ex-Hirase 618)
 ANSP, Syntypes, 80959
 Type Locality: Yaeyama Island, Japan (Hirase 618)

- decorata* Pilsbry, 1904. *Tornatina* ACTEOCINIDAE
 Proceedings of the Academy of Natural Sciences, Philadelphia, 56: 37, pl. 5, fig. 51
 =*Acteocina decorata* (Pilsbry)
 CM, 6 Paratypes, 62.9992
 ANSP, Holotype
 Type Locality: Hirado, Hizen, Kyushu, Japan

- floridanum* Clapp, 1918. *Carychium exiguum* ELLOBIIDAE
 The Nautilus, 31:73, pl. 8, figs. 4–6

=*Carychium floridanum* (Clapp)

CM, Holotype and 29 Paratypes, 46540 (ex-Simpson)

Type Locality: Snapper Creek Hammock, 8 mi. south of Miami, Florida

hachijoense Pilsbry, 1902. *Carychium*

ELLOBIIDAE

The Nautilus, 16:57

CM, 6 Syntypes, 62.15440 (ex-Hirase 946)

ANSP, Syntypes, 83,382, from Hirase's 946

Type Locality: Hachij-jima, Izu (Shizuoka Prefecture), Honshu, Japan

nana Bavay, 1908. *Pythia*

ELLOBIIDAE

Conchological Magazine (Kyoto), 2(1):1, 1 figure in text

CM, 6 Syntypes, 62.15741 (ex-Hirase 453—original syntype lot)

Type Locality: "Liu-Kiu" (=Ryukyu Islands, Okinawa Prefecture), Japan

nannodes Clapp, 1905. *Carychium*

ELLOBIIDAE

The Nautilus, 19:91, pl. 3, figs. 7-9

CM, Lectotype (selected by Brooks, 1936) and 60 Paratypes, 46539

ANSP, Paralectotypes, 107911

Type Locality: Monte Sano, 5 miles east Huntsville, Madison Co., Alabama, at 1600 feet

persubtilis Cooke, 1911. *Leptachatina*

AMASTRIDAE

Pilsbry's Manual of Conchology, (2)21:15, pl. 10, fig. 4

CM, 1 Paratype, 62.39798 (ex-Cooke, ex-BPBM 170119)

BPBM, Holotype, 170119

Type Locality: back of Waialua, Waianae Mts., Oahu, Hawaii

pessimum Pilsbry, 1902. *Carychium*

ELLOBIIDAE

Proceedings of the Academy of Natural Sciences, Philadelphia, 53:562

CM, 6 Syntypes, 62.15444 (ex-Hirase 729)

ANSP, Syntypes, 82481

Type Locality: Tane-ga-shima, Osumi, Kyushu, Japan (Hirase 729)

porphyrea Newcomb, 1853. *Achatinella*

AMASTRIDAE

Proceedings of the Zoological Society, London, 1853:136, pl. 22, fig. 16

=*Amastra* (*Paramastra*) *porphyrea* (Newcomb)

CM, 11 "Topotypes," 62.38656 (ex-Prime to Clapp)

Type Locality: Waianae, Oahu, Hawaii

stygium Call, 1897. *Carychium*

ELLOBIIDAE

American Naturalist, 37:387, pl. 10, figs. 6-7

CM, 10 Paratypes, 46538 (ex-Call)

ISU, Holotype

ANSP, Paratypes, 68147

Type Locality: Mammoth Cave, Kentucky

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———. 1923. The fauna of the Ardyn Obo For-

mation. American Museum of Natural History Novitates, no. 98:1–5.

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MATTHEW, W. D., W. GRANGER, AND G. G. SIMPSON. 1928. Paleocene multituberculates from Mongolia. American Museum of Natural History Novitates, no. 331:1–4.
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RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, in Pacific basin biogeography (J. L. Gressitt, ed.), Bishop Museum Press, Honolulu, Hawaii, xx + 450 pp.
- 5) Unpublished dissertation:
SMITH, J. P. 1976. Review of Eocene mammals. Unpublished Ph.D. dissert., University of California, Berkeley, 302 pp.
- 6) Book:
WHITE, M. J. D. 1961. The chromosomes. Methuen and Co., Ltd., London, 120 pp.
- 7) Journal articles with usual volume and issue number:
ANDERSON, W. I. 1969. Lower Mississippian conodonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

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THE CARNEGIE
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OSTEOARTHRITIS IN FOSSIL MARSUPIAL
POPULATIONS OF AUSTRALIABRUCE M. ROTHSCILD¹

Research Associate, Section of Vertebrate Fossils

RALPH E. MOLNAR²

ABSTRACT

The Australian Pleistocene marsupial population, as represented in the fossil record, demonstrates a limited distribution (affecting only two skeletal sites) but high frequency of osteoarthritis. Other forms of articular disease were notable by their absence. Osteoarthritis was noted in the proximal portion of the fourth metatarsal in macropods, and the astragalus in *Diprotodon* (both weight-stress bearing sites). The population frequency of osteoarthritis in weight-stress bearing regions in marsupials is similar to that in man.

INTRODUCTION

The taxonomy, distribution, and osteology of extinct Australian Pleistocene marsupials has been a subject of great interest (Raven and Gregory, 1946; Tedford, 1966). Previous studies of paleopathology have concentrated on man (Harcourt, 1971). Therefore, little is known about the history of non-human diseases, especially in Australian animals. Whereas isolated examples of pathology have been described, predominantly in captive animals, Horton and Samuel (1978) note the absence of previous population analyses. Attempts at population analysis have been limited to infectious disorders. Horton and Samuel (1978) reported a study of 2700 bones belonging to the kangaroo *Macropus titan*, dated at $26,600 \pm 650$ years before present. Examination of the descriptions and photographs of the pathologic specimens in that survey indicated that all identified lesions were infectious. Erosions, periosteal reactions, and other signs of osteomyelitis (bone destruction and/or new bone formation) and infectious arthritis were noted involving a fourth and fifth metatarsal, a metatarsal-tarsal joint, one femur, and two tibiae. With the exception of one possible example of osteoarthritis involving a fifth metatarsal, no credible osteoarthritis was noted. The specimen was described (Horton and Samuel, 1978:284) without illustration, as having "osteophytes surrounding the proximal articular surface and along the proximal third of the dorsal edge of the bone." This represented one of 55 metatarsals, for a population frequency of 1.8%. That example, however, was companion to a clearly infected fourth metatarsal, so the diagnosis of osteoarthritis must be considered unconfirmed.

Examination of isolated elements of available Pleistocene fauna in the collections of the Australian Museum, Sydney, and the Queensland Museum, Brisbane, revealed minimal pathology, with the exception of two groups for which sufficient numbers were available for population analysis. A combined 294 macropods

¹ The Arthritis Center of Northeast Ohio, 5701 Market St., Youngstown, OH 44512.

² P.O. Box 836, Fortitude Valley, Queensland 4006, Australia.

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(kangaroos) and 19 *Diprotodon* (an ox-like marsupial noted for its two forward projecting teeth), were available from the Sydney and Brisbane collections for definitive analysis of the frequency of bone pathology.

METHODS

Postcranial skeletons of macropods and *Diprotodon* in the collections of the Australian Museum and the Queensland Museum were examined for evidence of pathology. These collections represented disarticulated finds grouped by bone, since association by individual was not possible at the time.

Although it is known that the materials were collected during the nineteenth century from the Wellington Caves, Bingara, and Darling Downs, other than their Pleistocene age, all specifics with respect to site description and stratigraphy have been lost. The specimens are currently grouped according to bone, without attempt at identification below either the family Macropodidae or the genus *Diprotodon*. In the absence of any recent (i.e. twentieth-century) review of *Diprotodon*, no specific assignments can be confidently made.

RESULTS

The postcranial skeletons of 294 Pleistocene macropod fossils were examined for evidence of pathology. No alterations compatible with infection were identified in any of the post-cranial bones. Osteoarthritis, as manifested by osteophyte formation (bony overgrowth), was limited in distribution to the proximal articular margin of the fourth metatarsal. Pathology was notable by its absence from any other post-cranial bone. No evidence of eburnation (polished appearance secondary to grinding) could be identified. Osteophytes were noted in 78 of 294 fourth metatarsals examined (Fig. 1a). Radiologic examination for evidence of subchondral sclerosis (complication of osteoarthritis related to microfractures and healing) proved unrewarding, as density was uniform. Longitudinal section of a metatarsal revealed the ivory-like nature of the proximal portion of the fourth metatarsal (Fig. 1b). It should be noted that the fourth metatarsal is the weight- and shock-bearing bone involved in jumping. Though the affected metatarsals were not identified to species, all represented adult animals. Approximately one-third of the metatarsals were from individuals the size of giant kangaroos and so may well have represented *Macropus titan*. When bones were grouped by size, however, the frequency of osteoarthritis of the proximal fourth metatarsal was uniform and independent of size.

Examination of *Diprotodon* postcranial elements revealed only one pathologic specimen compatible with infection. Minimal subchondral erosive disease was noted in the astragalus. Sectioning the specimen through the erosion revealed a picture (thick reactive new bone formation) compatible with infection. Examination of the available bones representing the skeletons of 19 individuals revealed osteophyte formation involving the proximal portion of one tibia, the distal portion of one humerus, and five astragalar bones. As was noted for macropods, eburnation was notable by its absence. Radiologic examination proved unrewarding for identification of subchondral sclerosis.

DISCUSSION

Osteoarthritis is the most common form of bone-joint pathology affecting man (Rothschild, 1982; Engle et al., 1968). It presents as destruction and loss of articular cartilage, and is associated with remodeling of the subchondral bone (Rothschild, 1982). This remodeling basically takes three forms: 1) remodeling of the external surface of the bone results in overgrowth or osteophyte formation; 2) remodeling of the internal surface of the bone results in condensation and sclerosis of the



Fig. 1a.—Lateral view of proximal portion of fourth macropod metatarsal. Osteophytic spurring is noted as bony overgrowth at border of articular surface. 1b. Cross section of specimen illustrated in Fig. 1a. Osteophytic spurring is associated with a generalized ivory-like appearance of the bone.

underlying bone; and 3) occasional cyst formation in areas of relatively weakened bone. The ivory-like bone, noted above in the marsupial specimens examined, precluded cyst formation or sclerosis of the bone underlying the cartilagenous surface. The only recognizable manifestations of osteoarthritis in these marsupials would be osteophyte formation, which was observed only in select sites.

This study represents the first concerted analysis of arthritis in free-ranging marsupials, living or extinct. Bias inherent in sample selection must be regarded as minimal, as the entire population in the collections was examined. How representative of the endemic population is the population of specimens in the Sydney and Brisbane collections? As the collection logs and specimen descriptions are no longer available, this question is difficult to answer. It is, however, likely that the collected specimens represent the totality of excavation at the sites and, therefore, are representative of the bone bed in which they were found. Secondly, the osteoarthritis present is unlikely to be directly related to the animals' demise. Therefore, the collections probably do not reflect a population sampling selected on the basis of disease and can probably be considered representative of the endemic population.

Osteoarthritis was present in 27% of fossil Pleistocene kangaroos, independent of classification to species, but limited in distribution to the fourth metatarsal. The fourth metatarsal is the weight- and shock-bearing element of the lower extremity. Its ivory-like density appears to be a modification for facilitation of its handling of such stresses. The osteophytes probably affected the kangaroos only minimally, if at all, in their ability to function. Extent of osteophyte formation and clinical symptoms in man correlate only imprecisely. Thus it is impossible to be certain that these fossil kangaroos were in any way limited during life by their osteophyte development.

The unusual cranial appearance of *Diprotodon* is matched by that of its feet. The wrist joint is, at least in part, a ball-and-socket joint, the distal radius terminating in an articulating ball. The ball-and-socket forefoot may have offered relative protection from the occurrence of osteoarthritis, as forelimb involvement was demonstrable only in one distal humerus. The pronated posture of the rear foot, with the animal essentially walking on the side of its foot in a manner analogous to that of the giant ground sloth *Paramylodon*, may have been predisposed to astragalar involvement. The astragalus may represent the primary weight-

or stress-bearing site in *Diprotodon* and the osteoarthritis predominantly presenting at that site is as would be anticipated.

The disarticulated nature of the collection precludes age assessment beyond maturity, as age in marsupials is typically determined by teeth and their wear patterns. Osteoarthritis was common in Pleistocene macropods and *Diprotodon*, predominantly involving those joints which were at mechanical disadvantage. The 27% frequency of osteoarthritis in macropods and 26% frequency in *Diprotodon* are well within the frequency estimates for osteoarthritis in contemporary populations of man in the United States (Rothschild, 1982; Engle et al., 1968). Parallel development (e.g. of placental and marsupial bovine phenotypes) appears to have been complicated by parallel susceptibility to disease. It would be of interest to compare the incidence of osteoarthritis in fossil macropods with that of contemporary kangaroos.

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I would like to acknowledge the kindness of Alex Ritchie for allowing the senior author to examine specimens under his care and Larry Martin for specimen photography and critical review.

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DISTRIBUTIONAL RECORDS OF MAMMALS FROM THE
SOUTHWESTERN YUCATÁN PENINSULA OF MEXICOROBERT C. DOWLER¹

Research Associate, Section of Mammals

MARK D. ENGSTROM²

ABSTRACT

Records of mammals are reported for the Mexican states of Campeche and Tabasco on the Yucatán Peninsula. New distributional records include: *Uroderma bilobatum*, and *Micronycteris megalotis* from Campeche; and *Myotis elegans*, *Sylvilagus floridanus*, *Heteromys gaumeri*, and *Oryzomys fulvescens* from Tabasco. Additional information also is provided on the occurrence of *Cryptotis nigrescens* in Campeche and *Rhynchonycteris naso* in eastern Tabasco. Based on specimens reported in this study, the southwesternmost limit of the Yucatán Biotic Province, as it applies to mammals, is defined as that area of Tabasco north of the Sierra del Norte de Chiapas and east of the Río Usumacinta.

INTRODUCTION

The Mexican portion of the Yucatán Peninsula (see Fig. 1) is an area of mammalian endemism with a fauna that differs markedly from the rest of Mexico; however, few extensive field studies on mammals of this region have been conducted and distributional limits of this endemic fauna are not well understood. The most comprehensive studies of the peninsular mammalian fauna were a distributional monograph by Gaumer (1917) and a series of annotated checklists by Jones et al. (1973, 1974a, 1974b) and Genoways and Jones (1975). Other papers also have added to our knowledge of mammalian distributions on the Yucatán Peninsula, including those by Hatt (1938, 1953), Hatt and Villa-R. (1950), Jones and Lawlor (1965), Birney et al. (1974), Sanchez-H. et al. (1986), and McCarthy (1987). Our field work was designed to determine the distributional limits of mammals on the Peninsula and to examine the transition between the nuclear Middle American mammal fauna and that of the Yucatán Peninsula. Although the Mexican state of Tabasco often is not included in distributional studies of the Peninsula, our initial fieldwork indicated that the portion of Tabasco east of the Río Usumacinta and north of the Sierra del Norte de Chiapas contained a characteristic peninsular mammalian fauna. Consequently, this eastern section of Tabasco is considered herein to represent the southwesternmost extension of the Yucatán Biotic Province (for definition and discussion of this biotic province, see Goldman and Moore, 1945; Barrera, 1962).

Fieldwork for this study was conducted during July and August of 1980 and 1984. Specimens representing six new records for the Mexican states of Campeche and Tabasco are reported. Information also is included for two species previously reported from Campeche and Tabasco.

¹ Department of Biological Sciences, Fordham University, Bronx, New York 10458.

² Department of Biology, Angelo State University, San Angelo, Texas 76909.

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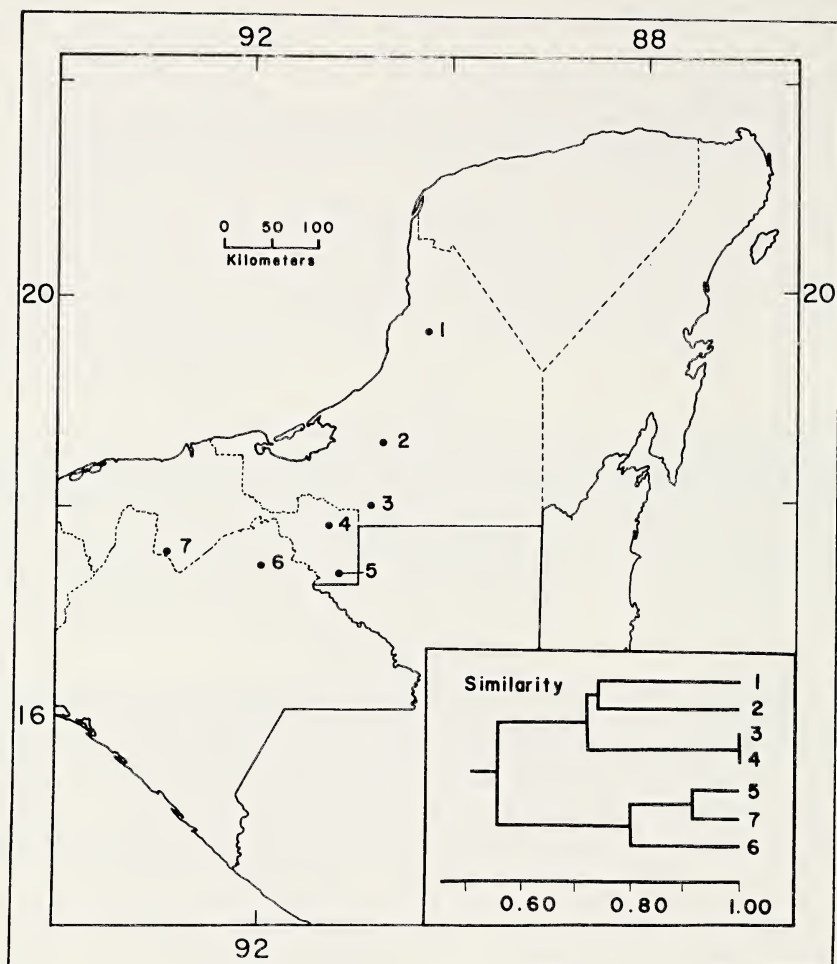


Fig. 1.—Map of the Yucatán Peninsula showing localities discussed in text. CAMPECHE: 1 = Edzna; 2 = 7.5 km W Escárcega; 3 = 11 km S Candelaria. TABASCO: 4 = 3.8 km SW Ruinas Acalán; 5 = 21–28 km SE Tenosique; 7 = Teapa. CHIAPAS: 6 = Palenque. Insert shows cluster analysis of localities based on the presence or absence of species of rodents (see Table 1 and discussion in text).

METHODS AND MATERIALS

Rodents were trapped using Sherman live traps and bats were obtained using mist nets. Specimens were preserved in fluid or prepared as standard museum study specimens and were deposited in the Angelo State Natural History Collections (ASNHC), Angelo State University, San Angelo, Texas; The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; or the Texas Cooperative Wildlife Collection, Texas A&M University, College Station, Texas. A representative series of specimens also was submitted to the Subsecretaría de Ecología, Dirección General de Flora y Fauna Silvestres, for deposit in Mexico. In the following accounts, external and cranial measurements, crown–rump lengths of embryos, and dimensions of testes are given in mm. Localities mentioned are shown in Fig. 1.

SPECIES ACCOUNTS

Cryptotis nigrescens mayensis

Specimens examined.—(1♀) Campeche: 7.5 km W Escárcega. A nonpregnant female was collected at an experimental forestry station (El Tormento) west of

Escárcega, on 24 July. The shrew was caught with a Sherman trap set in mature, transitional deciduous-evergreen forest. Other species caught in the same trapline included *Heteromys gaumeri*, *Ototylomys phyllotis*, *Peromyscus yucatanicus*, and *Oryzomys melanotis*.

Only one other *C. nigrescens* previously was reported from Campeche, an individual collected in 1911 from La Tuxpeña, near Champotón (Choate, 1970). Additional peninsular records of this species have been reported from the state of Yucatán (Gaumer, 1917; Hatt, 1953; Choate, 1970; Jones et al., 1974b).

Rhynchonycteris naso

Specimens examined.—(5: 3♀♀, 2♂♂) Tabasco: 3.8 km SW Ruinas Acalán (35 km N, 10 km E Tenosique). This species was first reported from southwestern Tabasco by Villa-R. (1966) at Río Puyacatengo, 15 km E Teapa, and our specimens represent the first from eastern Tabasco. The only other peninsular records of this species are from southeastern Quintana Roo, near the border with Belize (Jones et al., 1973).

Our specimens were netted over a tributary of the Río San Pedro on 15 July. This locality is near a small ruin site, approximately 25 km W of the village of San Pedro, and 35 km N, 10 km E Tenosique. The vegetation surrounding this area was secondary growth deciduous forest with no large trees, although a few trees of medium height lined the edge of the river. Our nets were set beneath the canopy of these trees over a relatively calm pool in a branch of the main river, near a group of small waterfalls. Each female carried a single embryo with crown-rump lengths of 12 and 25, respectively. One male had testes measuring 2 by 1. Other bats collected at this locality included *Pteronotus parnelli*, *Artibeus lituratus*, *Sturnira lilium*, *Carollia brevicauda*, *C. perspicillata*, *Desmodus rotundus*, and *Myotis elegans*.

Micronycteris megalotis mexicana

Specimens examined.—(1♂) Campeche: 7.5 km W Escárcega. This species previously has been reported from each state in the Mexican portion of the Peninsula except Campeche, although Jones et al. (1973) noted that it apparently was uncommon. We collected a single specimen on 30 July in a mist net set across a small, unpaved road in transitional deciduous-evergreen forest.

Uroderma bilobatum molaris

Specimens examined.—(7: 4♀♀, 3♂♂) Campeche: 11 km S Candelaria. This species previously was reported from southern Quintana Roo by Sanchez-H. et al. (1986) and McCarthy (1987) and our records are the first for the state of Campeche. We collected seven *U. bilobatum* in mist nets set across foot paths and over a small pool, in secondary growth transitional deciduous-evergreen forest in southwestern Campeche on 20–21 July. All females collected were pregnant and each carried a single fetus. Crown-rump lengths of fetuses from three females were 20, 21, and 25, respectively. Testicular measurements of two males were 5 by 3 and 4 by 2.

Although *U. bilobatum* has only recently been recorded from the Yucatán Peninsula of Mexico, our specimens along with those reported by Sanchez-H. et al. (1986) and McCarthy (1987), indicate that it probably is widely distributed in southern parts of the Peninsula.

Myotis elegans

Specimens examined.—(1♀) Tabasco: 3.8 km SW Ruinas Acalán (35 km N, 10 km E Tenosique). One nonpregnant female was collected in a mist net set over a tributary of the Río San Pedro on 15 July. This specimen represents the first record of the species for Tabasco and is only the second collected from the Peninsula. Jones et al. (1973) reported one *M. elegans* collected from 65 km S, 128 km E Escárcega, Campeche. Selected measurements for our specimen are: total length, 76; length of tail, 35; length of hind foot, 7; length of ear, 11; length of tragus, 6; length of forearm, 34; greatest length of skull, 12.8; zygomatic breadth, 8.2; breadth of braincase, 6.5.

Sylvilagus floridanus yucatanicus

Specimens examined.—(3: 2♀♀, 1♂) Tabasco: 3.8 km SW Ruinas Acalán (35 km N, 10 km E Tenosique). Cottontail rabbits were common at this locality, based on numerous sightings during our field work. Our specimens were shot by a local hunter on 14 July. One of the two females collected had three embryos that measured 80 and the male had testes measuring 32 by 17.

S. floridanus has not previously been recorded from Tabasco (Ramírez-Pulido et al., 1986) and the range map for the species depicted in Hall (1981) indicated a distinct hiatus in Tabasco between the distributions of *S. f. yucatanicus* in Yucatán and Campeche, and the two nearest subspecies, *S. f. russatus* in southern Veracruz and *S. f. chiapensis* in the central highlands of Chiapas and Guatemala. Nelson (1909) distinguished these three subspecies mainly on the basis of coloration and size. *S. f. yucatanicus* and *S. f. chiapensis* were distinguished from *S. f. russatus* by their larger external and cranial size (particularly total length and length of ear). *S. f. yucatanicus* was distinguished from *S. f. chiapensis* by paler coloration, proportionately larger auditory bullae (diameter averaging greater than 11 in *S. f. yucatanicus* and less than 10 in *S. f. chiapensis*) and pronounced fusion of the postorbital processes with the cranium, in the former. Our specimens were relatively pale (particularly in the diagnostic rear of the hind legs), were large externally and cranially, had relatively large auditory bullae (mean diameter = 11.3), and the postorbital processes were fused with the cranium in each specimen. Accordingly, although our specimens are approximately equidistant among the currently recognized geographic ranges of the three subspecies, they are clearly assignable to *S. f. yucatanicus*. Selected measurements of the three specimens from Tabasco, two adult females followed by one adult male, respectively, are as follows: total length, 450, 457, 440; length of tail, 40, 47, 37; length of hind foot, 92, 96, 96; length of ear, 64, 66, 66; greatest length of skull, 79.4, 81.3, 78.4; zygomatic breadth, 37.4, 36.4, 35.6; mastoid breadth, 36.4, 36.8, 36.6; length of maxillary toothrow, 14.9, 14.2, 14.8; diameter of bulla, 11.0, 11.8, 11.0.

Oryzomys fulvescens mayensis

Specimens examined.—(1♀) Tabasco: 3.8 km SW Ruinas Acalán (35 km N, 10 km E Tenosique). A subadult female was collected on 17 July in secondary deciduous forest bordering overgrown but grazed pasture. The specimen was pregnant with four embryos measuring 12. Other species of rodents taken at this locality included *Heteromys gaumeri*, *Sigmodon hispidus*, *Oryzomys melanotis*, *O. couesi*, *Ototylomys phyllotis*, and *Rattus rattus*. Jones et al. (1973) recorded specimens of this species from Campeche and Yucatán, but this specimen is the first reported for the state of Tabasco.

O. f. mayensis was described from Campeche and Yucatán by Goldman (1918) as distinct from adjacent populations of *O. f. fulvescens*, based on paler coloration and narrower skull (particularly zygomatic breadth) of the former. Comparison of the specimen from Tabasco with adult specimens of *O. f. mayensis* from near Candelaria in southern Campeche (1♂) and *O. f. fulvescens* from near Palenque in northeastern Chiapas (1♀, 2♂♂) in the ASNHC revealed little variation in color among the specimens. Of those examined, the individual from Tabasco is slightly paler middorsally, due to a lack of suffusion of the dorsum with reddish hairs. The skull of the specimen from Tabasco also is among the smallest of the series, although size variation among these specimens might owe to differences in age. Based primarily on relatively narrow zygoma, we tentatively assign the specimen from Tabasco to the peninsular subspecies. Selected external and cranial measurements of the three specimens from 6.6 to 9.5 km S Palenque, Chiapas (one adult female, followed by two adult males), the adult male from 11 km S Candelaria, Campeche, and the subadult female from Tabasco are, respectively: total length, 186, 186, 192, 172, 166; length of tail, 106, 111, 109, 99, 93; length of hind foot, 21, 22, 22, 21, 21; greatest length of skull, 26.8, 27.1, 26.9, 25.6, 26.0; length of rostrum, 7.2, 7.7, 7.6, 6.9, 6.6; zygomatic breadth, 11.4, 11.4, 11.7, 11.2, 11.0; breadth of braincase, 9.8, 9.7, 10.3, 10.1, 10.3.

Heteromys gaumeri

Specimens examined.—(11: 7♀♀, 4♂♂) Tabasco: 3.8 km SW Ruinas Acalán (35 km N, 10 km E Tenosique). This species is endemic to the Yucatán Peninsula. Our specimens from Tabasco represent the first records for the state and the southwesternmost locality at which the species has been collected (see Engstrom et al., 1987). *H. gaumeri* were trapped in secondary deciduous forest and brushy areas near a tributary of the Río San Pedro. Of seven females collected on 15 and 16 July, none were pregnant. Testes measurements for two males collected on those dates were 17 by 10 and 6 by 3. Other rodents taken at this locality were listed under the account for *Oryzomys fulvescens*.

DISCUSSION

Previous authors who delineated the Yucatán Biotic Province based all or in part on mammalian distributions (Goldman and Moore, 1945; Barrera, 1962), usually included extreme eastern Tabasco within the province (although this area was not included in the checklists of Yucatán mammals by Jones et al., 1973, 1974a, 1974b, and Genoways and Jones, 1975). However, there are few distributional records of mammals (particularly rodents) from this portion of Tabasco and inclusion of this area in the Yucatán Biotic Province based on mammalian distributions was conjectural.

Initially, this study was designed to examine the transition between the southwestern peninsular mammalian fauna and that in nuclear Middle America. Localities reported herein (with reference to place names Escárcega and Candelaria, Campeche; and Acalán, Tabasco) and additional localities represented in our collections (near Edzna, Campeche; Tenosique and Teapa, Tabasco; and Palenque, Chiapas) approximate a transect from northern Campeche southwest to Tabasco and northern Chiapas (Fig. 1). We calculated similarities for all pairwise comparisons among these seven localities based on the presence or absence of species of rodents (Table 1), using the similarity coefficient of Baroni-Urbani and Buser (1976). Cluster analysis using the unweighted pair group method based on arith-

Table 1.—Presence or absence of species of rodents used to calculate similarity coefficients among seven localities from the Yucatán Peninsula of Mexico. Locality numbers are defined in Fig. 1.

	Localities						
	1	2	3	4	5	6	7
<i>Heteromys gaumeri</i>	1	1	1	1	0	0	0
<i>H. desmarestianus</i>	0	0	0	0	1	1	1
<i>Oryzomys couesi</i>	0	1	1	1	0	1	1
<i>O. melanotis</i>	1	1	1	1	1	1	1
<i>O. fulvescens</i>	0	0	1	1	0	1	0
<i>Tylomys nudicaudus</i>	0	0	0	0	0	1	0
<i>Ototylomys phyllotis</i>	1	1	1	1	1	1	1
<i>Reithrodontomys gracilis</i>	0	1	0	0	0	0	0
<i>Peromyscus leucopus</i>	0	1	0	0	0	0	0
<i>P. yucatanicus</i>	1	1	0	0	0	0	0
<i>P. mexicanus</i>	0	0	0	0	1	1	1
<i>Sigmodon hispidus</i>	1	1	1	1	1	1	1

metic averages (UPGMA; Sneath and Sokal, 1973) was performed on the resulting matrix to depict faunistically similar subsets of localities (also see Lee, 1980). This analysis was restricted to data from rodents because members of this order comprise the majority of non-insular, endemic species characteristic of the peninsular fauna and because these taxa were best represented in our (and previous) collections.

In the UPGMA analysis (Fig. 1), the principal distinction among localities was between samples collected in the foothills of the Sierra del Norte de Chiapas (near Palenque, Teapa, and Tenosique) and those to the north and east (near Acalán, Candelaria, Escárcega, and Edzna). Localities in the Sierra del Norte de Chiapas were characterized by the presence of non-peninsular rodent species (e.g. *Peromyscus mexicanus* and *Heteromys desmarestianus*), widespread Middle American taxa, and the absence of Yucatán endemics (e.g. *Peromyscus yucatanicus* and *Heteromys gaumeri*). Localities to the north and east of this mountain range were characterized by the presence of at least some taxa endemic to the peninsula (e.g. *H. gaumeri*), widespread Middle American species, and absence of non-peninsular species.

Differentiation of the species composition of rodent communities between these groups of localities parallels a decrease in rainfall and change in plant communities at the northern margin of the Sierra del Norte de Chiapas. For example, annual precipitation at San Pedro, 10 km west of our collecting site near Acalán, is approximately 1500 mm, whereas that near our collecting localities southeast of Tenosique is approximately 2200 mm (Garcia, 1973). Primary vegetation near Acalán is medium-height, sub-perennial sub-deciduous forest whereas that southwest of Tenosique is tall, perennial rain forest. Although the distance between these localities is only 50 km (see Fig. 1), Acalán has a typical peninsular rodent fauna (the principal exception being the absence of *P. yucatanicus*, which has not been collected at any locality southwest of Escárcega) and clusters with localities to the north, whereas our sites southeast of Tenosique had a more typical nuclear Middle American fauna and cluster with other localities in the Sierra del Norte de Chiapas, to the west.

Based on the distributions of rodent communities from this study we define the southwesternmost limit of the Yucatán Biotic Province, as it applies to mam-

malian distributions, as that area of Tabasco north of the Sierra del Norte de Chiapas and, based on previous studies (see Hall, 1981), west of the Río Usumacinta. This boundary closely parallels that proposed by Barrera (1962), based on the distributions of terrestrial and aquatic vertebrates.

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AFRO-MONTSERRATIAN CERAMICS FROM
THE HARNEY SITE CEMETERY,
MONTSERRAT, WEST INDIESJAMES B. PETERSEN¹

Research Associate, Section of Anthropology

DAVID R. WATTERS

Assistant Curator, Section of Anthropology

ABSTRACT

A small sample of Afro-Montserratian ceramics was recovered from the Harney site where 17 Black slaves were excavated from an unmarked 18th century cemetery on the island of Montserrat, West Indies. The 20 fragmentary sherds, representing eight ceramic vessels, were recovered from the fill above three of the in situ burials and from disturbed contexts. The sherds probably were inadvertent inclusions in the graves rather than purposefully emplaced grave goods. Dated minimally to the latter half of the 18th century on the basis of associated artifacts, these ceramics are described using vessel lot and attribute based methods. This detailed documentation establishes the relationship between the Harney site ceramics and other similar samples derived from a common African tradition of coil-built, open hearth-fired ceramic manufacture in the West Indies.

INTRODUCTION

Parts of 17 skeletons and an assemblage of historical artifacts were recovered during a six-day salvage excavation in 1979 at the Harney site (MS-A-H4), Montserrat, West Indies (Fig. 1). Although construction activities for a house foundation had caused considerable damage to this unmarked and unrecorded cemetery site, a crew of volunteer archaeologists was able to recover portions of ten skeletons from in situ graves during the salvage project. Osteological analysis (Mann et al., 1987) of the skeletons from the graves and additional bones removed by the construction workers as well as analysis of the artifacts (Watters, 1987) indicate the Harney site was a slave cemetery in use at least during the latter 18th century.

Artifacts found at the site included nails, other metal items, clay pipes, glass, European earthenware and stoneware ceramics, and 20 unglazed, relatively coarse tempered sherds. The unglazed sherds are of particular concern in this paper because the authors believe them to be the remains of pottery made on Montserrat by slaves. The sherds were categorized previously as "colonoware" to differentiate them from the ceramics obviously imported from Europe (Watters, 1987:305-307). Colonoware was used in a somewhat generic sense to distinguish locally made ceramics from imported ones.

The 20 unglazed sherds are now re-designated as "Afro-Montserratian" ware. The new designation is applied to these sherds in consideration of terminological convention and consistency among Caribbean regional researchers. It has the advantage of identifying the group that made the pottery and the island on which it was made. Usage of the prefix "Afro" implies that the pottery was made by

¹ Archaeology Research Center, Department of Social Sciences & Business, University of Maine at Farmington, Farmington, Maine 04938.

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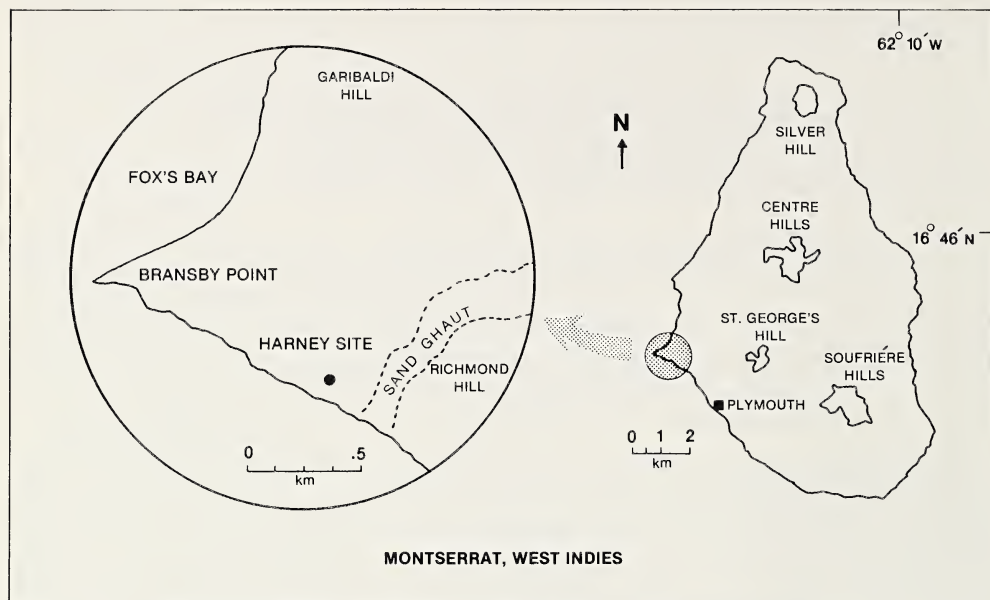


Fig. 1.—Location of the Harney site on the west coast of Montserrat.

Africans or their descendants in a distinctive tradition different from other locally manufactured ceramics that may have been made by Europeans or their descendants. The latter group most notably includes indentured servants who were present on Montserrat in considerable numbers in the period of initial European colonization. Afro also serves to distinguish this earthenware pottery from ceramics made by Amerindians during the colonial period.

Whether the ceramics made by these different groups really can be distinguished has yet to be verified fully, a point that the authors recognize as a valid problem needing further study. Differentiation of pottery made by distinctive ethnic groups has been previously attempted by historical archaeologists. For example, Noël Hume (1962) described "Colono-Indian" pottery in Virginia on the basis of his suspicion that some pottery in historical sites showed European morphology combined with apparent non-European (probably Indian) attributes, such as shell temper and "hand-made" manufacture. More recently, Ferguson (1980) and Deagan (1987:103–104), among others, have suggested that "Colono Ware" ceramics can be attributed to both Indian and Black potters. In a sense then, colonoware has become a less specific or increasingly generic term in North American historical archaeology through time.

In the West Indies, various researchers have struggled with the terminology problems of the locally made, colonial period ceramics. Colonoware and "folk pottery" have been used as generic labels for the colonial ceramics. However, even in those instances the implicit assumption has been that the ceramics were made by Black potters. More recently, designation of Black-made ceramics has followed an "island specific" attribution system. Thus, Gartley (1979) applied "Afro-Cruzan" to pottery from St. Croix, Nicholson (1983, 1984, 1985) designated "Afro-Antiguan" pottery on Antigua, and Armstrong (in press) adopted "Afro-Jamaican" to describe his coarse earthenware historical ceramics from Jamaica.

The contention that the pottery described here as Afro-Montserratian was made



Fig. 2.—View of the Harney site, facing west, showing trenches excavated by the construction workers.

by Black slaves hinges on three factors: 1) the racial identity of the Harney site skeletons; 2) the relationship of the sherds to those skeletons; and most importantly, 3) the nature of the ceramic remains as discussed in detail below.

THE CEMETERY

Circumstances surrounding the excavation of the Harney site and reasons for the site's disturbance (Fig. 2) and incomplete condition of most of its skeletons are found in Watters (1987). Despite the constraints of the salvage project and the limits of the archaeological data, the Harney site was determined to be a Black slave cemetery.

The best direct evidence for the racial designation comes from the only two skulls found in in situ burials (skeletons 4 and 7), both of which have been determined to be Black individuals (Mann et al., 1987: table 1). Among the bones removed from their primary context by the construction workers, one maxilla (bone 19) can reliably be designated Black, while another maxilla (bone 7) is a probable Black (Mann et al., 1987: table 2). Primary race estimates were based on criteria exhibited in the skull. Since all of the other Harney site skeletons consist mainly of post-cranial bones, Mann et al. (1987) have listed the other skeletons as "race indeterminate." However, they do note that "the general contour of most femora (anteroposteriorly) is flattened, furthering suggesting Black individuals" (Mann et al., 1987:335). In every instance where the skull was complete enough to permit thorough examination, the designation as Black was based on the presence of several Negroid cranial traits.

Mann et al. (1987) provide further support of the contention that the Harney site burials represent Black slaves. This includes identification of various patho-

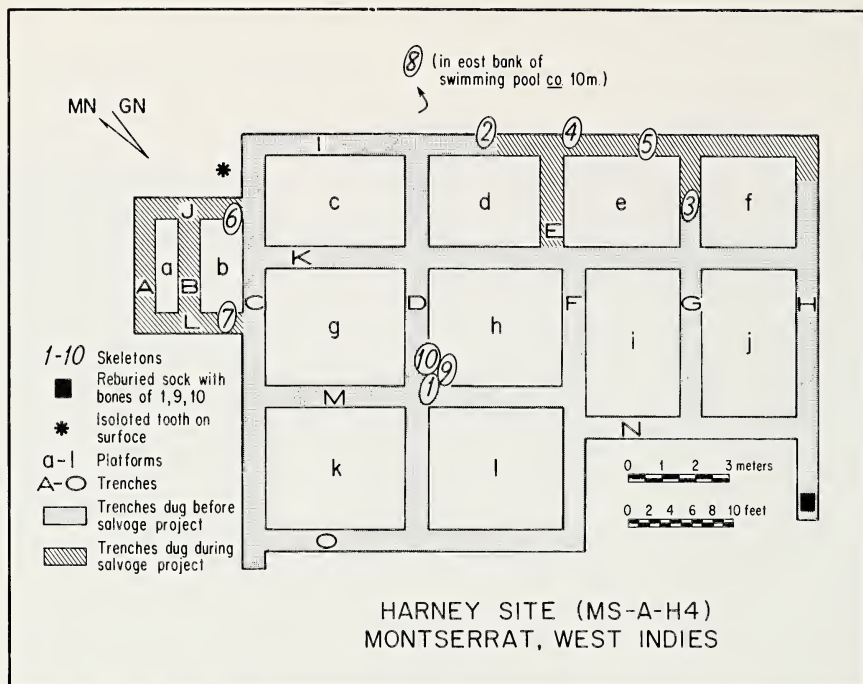


Fig. 3.—Plan view of the Harney site showing locations of the in situ skeletons in relation to the grid.

logical conditions, such as enthesopathies, osteoarthritis, anemia, malnutrition, and a high incidence of fractures, that have been found in other slave skeletal populations. Also of interest, each individual for which phalanges and metacarpals were recovered showed evidence of well developed muscle attachment areas as one could expect for arduous grasping activities associated with slavery, such as hoeing and chopping sugar cane.

At the Harney site, the interred individuals most likely were slaves rather than freedmen based on the probable period of use of the cemetery in the latter 18th century. This period is well before abolition of slavery and emancipation of slaves in the British West Indies which occurred in the 1830s (Parry and Sherlock, 1971). One dated artifact, a Turlington Balsam of Life bottle inscribed 1751, and pipe stems and European ceramics further support attribution of the cemetery to the latter 18th century (Watters, 1987).

Finally, although they form a less compelling argument, some aspects of the burials themselves, such as placement in unmarked graves and the lack of grave goods or clothing accoutrements, might be inferred as supporting the designation as slaves.

DISTRIBUTION OF AFRO-MONTSERRATIAN SHERDS

The 20 sherds were recovered adjacent to or from the fill above three of the in situ skeletons (ten sherds) and from backdirt piles that had been bulldozed from the site before the archaeologists arrived (ten sherds). Although 19 sherds were originally classified as "colonoware" (Watters 1987: tables 2 and 3), this analysis includes an additional sherd among the "Afro-Montserratian" ceramics because

Table 1.—*Distribution of excavated and disturbed Afro-Montserratian sherds at the Harney Site.*

Provenience	Vessel ^a	Body	Rim	Total	FSN ^b	Sex	Age
Excavated							
Skeleton 1 (+9?)	1	6	1	7	41 to 44 46 to 48	F	50+
	2	1	—	1	45		
Skeleton 3	1	1	—	1	74	M	35-45
Skeleton 6	3	1	—	1	88	F	18-35
Disturbed (all from backdirt)	4	3	—	3	5, 7, 8	—	—
	5	2	1	3	1, 6, 9	—	—
	6	2	—	2	3, 4	—	—
	7	1	—	1	2	—	—
	8	—	1	1	10	—	—

^a Vessels 1 and 2 were found with skeleton 1; seven sherds from vessel 1 were found with skeleton 1 and one sherd with skeleton 3.

^b FSN are Field Specimen Numbers applied to the 20 sherds; FSN are preceded by MS-A-H4 (site designator for the Harney site).

it more closely resembles these ceramics than European ceramics (as will be discussed at length below).

The distribution of the ten Afro-Montserratian sherds found in proximity to three of the in situ skeletons (Fig. 3) is of interest here. In one case, skeleton 6, a small sherd was found immediately adjacent to the bones. Skeleton 6 is a female between the age of 18 and 35 (Mann et al., 1987: table 1). A single sherd was found in the soil overlying the lower extremities of skeleton 3, the only part of that skeleton not destroyed by construction work. Skeleton 3 is a male between 35 and 45 years old at death (Mann et al., 1987: table 1).

Eight Afro-Montserratian sherds were recovered from the soil above skeleton 1. However, skeleton 1, for which only the lower articulated body was preserved, was not the only skeleton in the grave. Adjacent to and underlying skeleton 1 were bones from skeleton 9, a disarticulated skeleton whose bones had been scattered in the historic past rather than through modern disturbance (Watters, 1987:299). Skeleton 9 was interred before skeleton 1. Gravediggers for skeleton 1, upon finding skeleton 9 already in place, pushed aside its bones to make room for the new burial and in doing so created the disordered condition. The eight Afro-Montserratian sherds could have been included in the fill for either burial. Skeleton 1 is a female aged at 50+ years; skeleton 9 is a male aged at 40+ years (Mann et al., 1987: table 1).

In the sections that follow, few distinctions are made between the ten sherds found in the graves and those from the backdirt piles because they are all treated as one sample for descriptive purposes. However, provenience distinctions are presented in Table 1, with information on the age and sex of the skeletons.

It is unlikely that the ten sherds found in the graves were originally emplaced as grave goods in the sense that they were purposefully deposited. On the basis of their fragmentary condition and context, it is more logical to conclude that the Afro-Montserratian sherds were inadvertent introductions into the fill being shoveled into the grave after the corpse had been emplaced. The argument for unintentional introduction of these sherds is supported by an interesting finding. A single vessel (see discussion under Analytical Methods) is represented by eight sherds, seven of which were found with skeleton 1 and one with skeleton 3. These

skeletons were separated by a distance of almost 10 meters, so there is no conceivable way a single vessel could have been intentionally deposited as an intact grave good in two different graves.

We contend that the Afro-Montserratian ceramics were made by Black slave potters on Montserrat for five reasons:

First, the sherds were introduced into each grave as it was being filled. These sherds may have been lying on the ground surface of the cemetery, perhaps having been left there from previous burial services, or they may have been the remains of vessels brought to the site by mourners during the burials. In the former case, the sherds may have predated the burials, while in the latter they may have been contemporaneous. Whether the sherds predated or were contemporaneous with the burials, the action that introduced them into the graves immediately after placement of the corpse was essentially a simultaneous action.

Second, it is very unlikely that the sherds are older Amerindian ceramics that were inadvertently introduced into the graves and, in turn, were misidentified as Afro-Montserratian sherds. There is no evidence of Amerindian artifacts within the excavations, in the backdirt piles, or even in the general vicinity of the site.

Third, all of the artifacts at the Harney site are historic ones, and those with some temporal control indicate a latter 18th century time span. There are no diagnostic artifacts that are significantly earlier or later.

Fourth, the Afro-Montserratian sherds differ radically from European earthenwares and stonewares found at the Harney site, and they differ somewhat from Amerindian sherds known from other sites (see Ceramic Vessels section below).

Fifth, there are recognized similarities between the Harney site pottery sherds and other pottery made by Blacks (slaves and freedmen) in the West Indies and North America (e.g., Armstrong, in press; Deetz, 1977). These similarities are discussed further at the end of this paper.

ANALYTICAL METHODS

A standard vessel lot analysis of the Harney Afro-Montserratian ceramics was conducted using methods developed in a variety of prior ceramic analyses (e.g., Petersen, 1980, 1985; Petersen and Power, 1985). Vessel lot analysis is essentially a descriptive reconstruction of once extant vessels given the limitations of their preservation. It enables definition of the minimum number of individual vessels represented within a given sample and further provides detailed ceramic data to document these vessels and to allow subsequent comparison with other samples. Vessel lot analysis can be also useful in the correlation of depositional or natural strata, cultural features and other provenience units for a specific archaeological site since assignment of ceramic specimens to one or another ceramic vessel, like actually conjoining sherds, establishes their common origin and thus their precise contemporaneity.

Eight ceramic vessels have been defined from the 20 sherds recovered from the Harney site (Fig. 4 and 5). The sherds have a total weight of 277.0 grams. The eight vessels are described below by various attribute categories, or modes (Rouse, 1939:11–12, 1960). These ceramic modes represent potentially diagnostic attributes that *may* be discrete in temporal, spatial, and/or cultural dimensions.

All specimens were initially cleaned and catalogued by Watters. Each specimen was then analyzed by Petersen using a variable power binocular microscope (10×–25×) and macroscopic observation. All measurements were taken with needle-nose calipers accurate to 0.05 mm and all color values were recorded using Munsell soil color charts.

CERAMIC VESSELS

Temper. —The temper in the eight defined vessels is very similar (Table 2; Figs. 6–9). It is typically heterogeneous, fine to medium sized and dominated by angular to subangular quartz with lesser quantities of tourmaline and amphibole/hornblende on the basis of residual crystal structure, a pink or white mineral, certainly



Fig. 4.—Ceramic sherds recovered from fill around in situ skeletons at the Harney site. Numbers 1–3 correspond to vessel designations.

feldspar, and magnetite. The minerals were combined in these relative proportions with three exceptions: vessel 2, which exhibits fewer temper constituents than the other vessels, with feldspar predominating over quartz and tourmaline (Fig. 7A); vessel 6, which exhibits predominant amphibole/hornblende (Fig. 6D and 9A); and vessel 8, which exhibits predominant tourmaline temper (Fig. 6F and 9B).

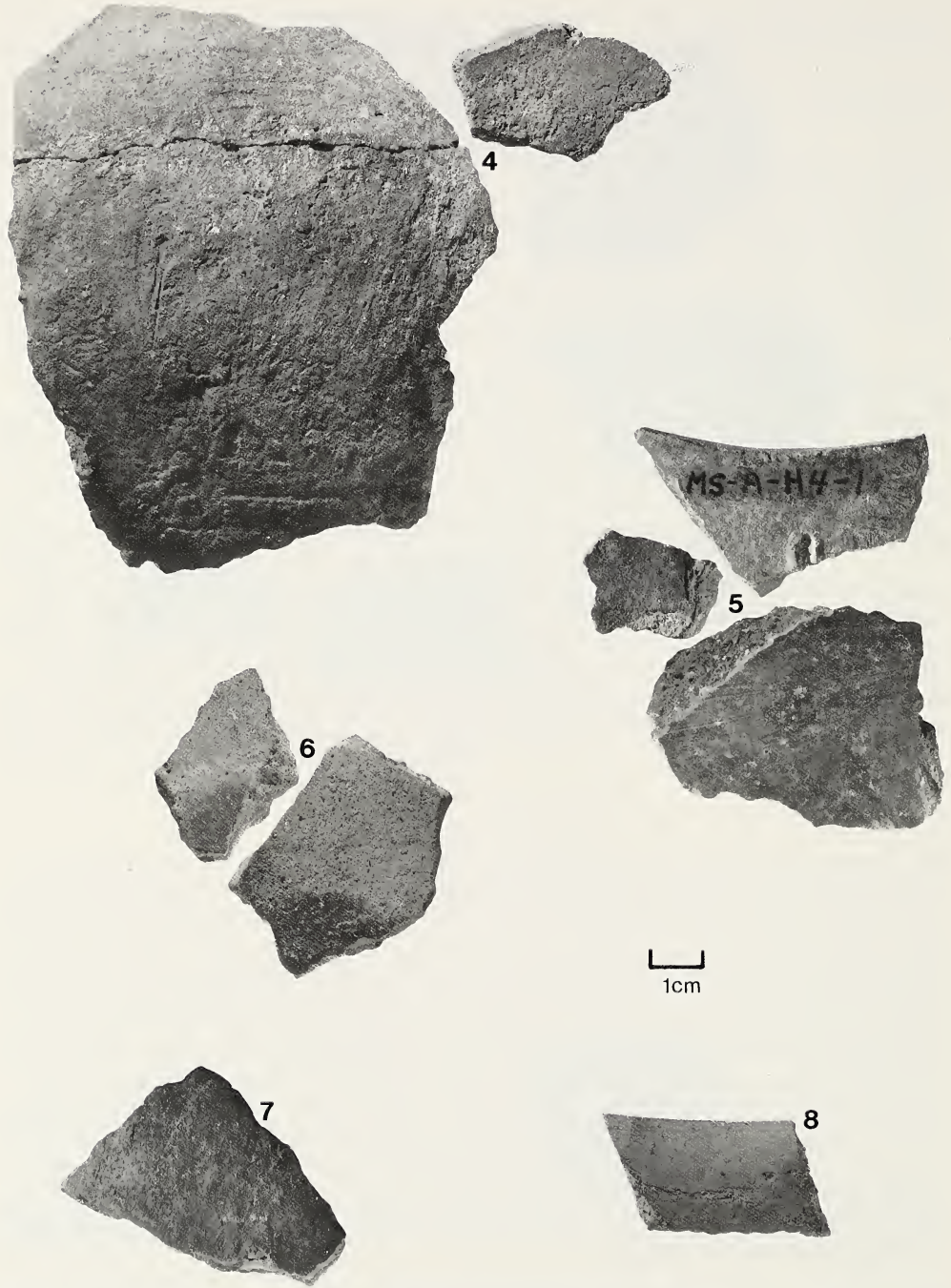


Fig. 5.— Ceramic sherds recovered from disturbed contexts at the Harney site. Numbers 4–8 correspond to vessel designations.

Table 2.—*Harney site Afro-Montserratian ceramic vessel attributes.*

Vessel designation Number of specimens	1 (8)	2 (1)	3 (1)	4 (3)	5 (3)	6 (2)	7 (1)	8 (1)
Temper								
Quartz	X	X	X	X	X	X	X	X
Tourmaline	X	X	X	X		X	X	X
Amphibole/Hornblende	X			X	X	X	X	X
Feldspar	X	X	X	X	X	X	X	X
Iron concretion	X							
Other	X	X	X	X	X	X	X	X
Texture								
Fine body	X				X			
Medium body		X	X	X		X	X	X
Extrusive		X	X	X		X	X	X
Not extrusive	X				X			
Moderate consolidation		X						
Thorough consolidation	X		X	X	X	X	X	X
Blocky angular fractures	X	X	X	X	X	X	X	X
Vesicles	X		X	X	X		X	
Manufacture								
Coiled	X	X		X	X	X	X	X
Unknown			X					
Coil size (X) (mm)	9.65	9.65		12.13	11.00	10.20	11.40	12.15
	X	X		X	X	X	X	X
	6.98	6.53		6.75	7.95	7.80	8.00	10.05
Surface finish								
Smoothed exterior	X	X	X		X	X	X	X
Smooth irregular exterior				X				
Smoothed lip	X				X			X
Unknown lip		X	X	X		X	X	
Smoothed interior	X	X	X	X	X	X		X
Smooth irregular interior							X	

Much of the quartz and some of the tourmaline and hornblende seems to be a fine sand, generally less than 0.60 mm in size, whereas the feldspar and most of the hornblende is medium ($\geq 1.00 \leq 3.00$ mm), or coarse (> 3.00 mm) in size. The largest feldspar constituents are less than 6.00–7.00 mm in size. The feldspar and some of the quartz, tourmaline, and amphibole/hornblende were clearly derived from rocks of igneous origin. These temper constituents typically exceed 50% of the total volume of the ceramic paste, with three exceptions. The exceptions, vessels 2, 3 and 5, exhibit temper which is approximately 35–50% of the total volume of the paste.

Vessel 1 (Fig. 6A) includes sparse amounts ($< 5\%$) of fine to medium size inclusions of iron concretions which are the likely result of the decomposition of the magnetite. All vessels show variable size white tuff lithic fragments, of which several, notably vessels 4 and 7, show large obvious inclusions (Fig. 6B and 6E). The iron concretions are less than 2.00 mm, while the white tuff lithic fragments are as large as 8.30 mm.

In sum, the identified temper constituents and inclusions suggest a probable local origin on Montserrat. In fact, these materials exhibit comparable weathering, composition, and age. It seems almost certain that the temper was derived from

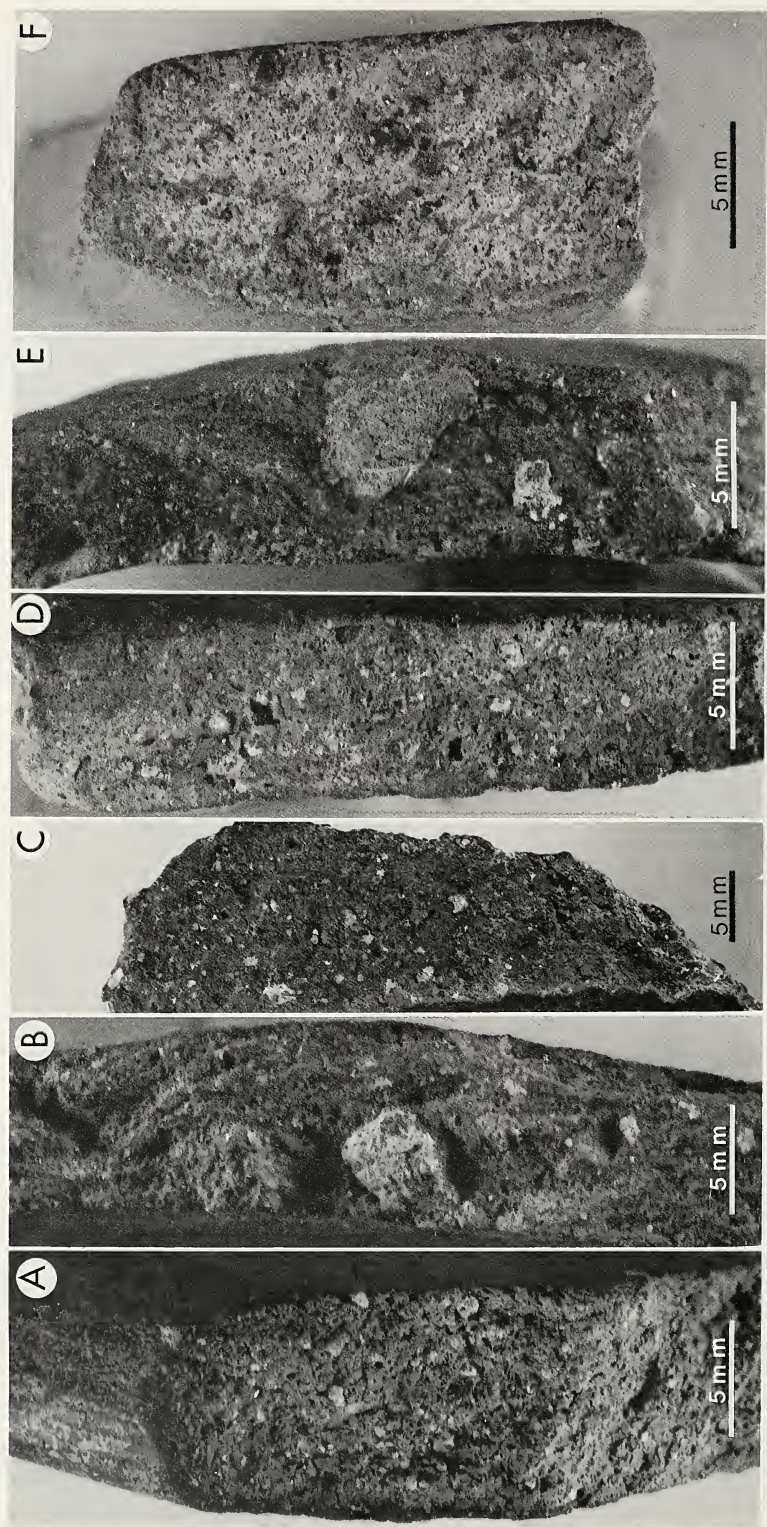


Fig. 6.—Ceramic sherd cross sections on broken edges showing temper constituents and internal laminations. A. Cross section of vessel 1 rim sherd (FSN 48) showing predominant quartz and feldspar temper. B. Cross section of vessel 4 body sherd (FSN 7) showing large white tuff fragment and other temper constituents, and individual coils. C. Cross section of vessel 5 body sherd (FSN 6) showing predominant quartz and feldspar temper. D. Cross section of vessel 6 body sherd (FSN 4) showing predominant quartz and feldspar, and tourmaline temper along a coil fracture. E. Cross section of vessel 7 body sherd (FSN 2) showing large white tuff fragment, predominant quartz and feldspar temper, and structural laminations. F. Cross section of vessel 8 rim sherd (FSN 10) showing predominant tourmaline, quartz and feldspar, and coil fracture on lower edge.

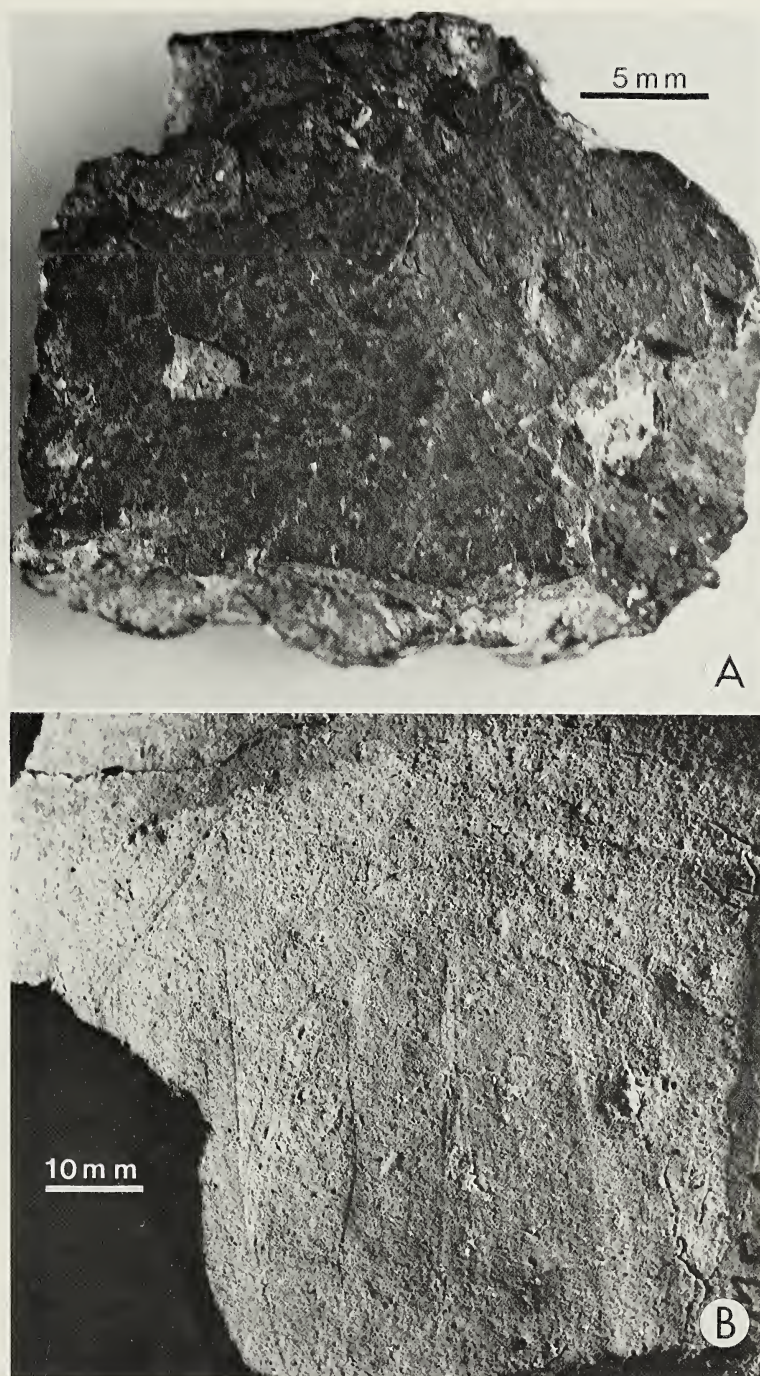


Fig. 7.—Ceramic sherd exterior and interior surfaces. A. Exterior surface of vessel 2 body sherd (FSN 45) showing predominant feldspar temper, white tuff fragment, smooth irregular finish, and coil fractures on upper and lower edges. B. Interior surface of vessel 4 body sherd (FSN 7) showing extrusive predominant quartz and feldspar temper, and smooth finish with plastic flow.



Fig. 8.—A. Interior surface of vessel 5 rim sherd (FSN 1) showing smooth surface with extensive plastic flow. B. Exterior surface of vessel 5 rim sherd (FSN 1) showing detail of fragmentary incised decoration.

the white rock “shoal,” or partially welded tuff that is locally present in the Bransby Point area where the Harney site is located (Watters, 1987:303).

Unfortunately, few precise comparative temper data are available for other Black-made ceramics or similar wares from the West Indies and North America (e.g., Armstrong, in press; Bullen and Bullen, 1972:148–149, Plates 34c–e; Deetz, 1977:147–148; Ferguson, 1980; Gartley, 1979; Handler, 1963a; Handler and Lange, 1978:140–144; Moran et al., 1982:92–93; Wheaton and Garrow, 1985:

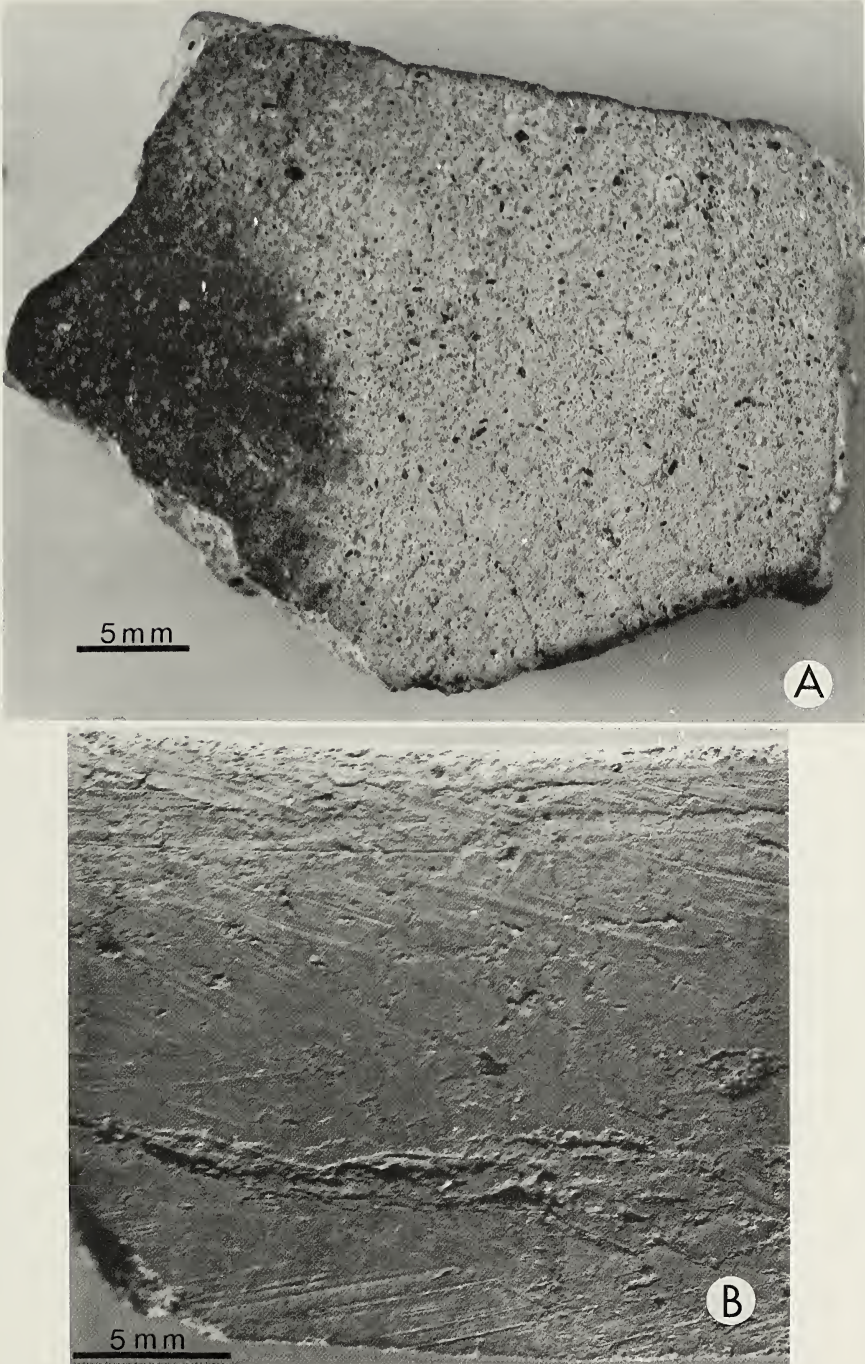


Fig. 9.—A. Exterior surface of vessel 6 body sherd (FSN 4) showing dark firing cloud, predominant amphibole/hornblende temper, and coil fracture on upper edge. B. Exterior surface of vessel 8 rim sherd (FSN 10) showing sparse extrusive quartz, feldspar, and tourmaline temper, smooth irregular finish with plastic flow, and coil fracture on lower edge.

248–249). Of these, temper in the Harney ceramics generally seems most similar to samples from the Virgin Islands, Jamaica and St. Vincent (Armstrong, in press; Bullen and Bullen, 1972; Gartley, 1979), but few of these have been thoroughly described. Personal examination of the only three “nonwheel made” sherds from the Newton slave cemetery on Barbados (Handler and Lange, 1978:141) revealed a heterogenous mixture of apparent temper comparable to the Harney specimens, although including different constituents.

There are few temper data available for the more commonly analyzed Amerindian ceramics from the West Indies. It may be significant, however, that the Harney site ceramics exhibit generally similar temper constituents to recently analyzed ceramics of unequivocal Amerindian origin from the Trant’s site on Montserrat and Fountain Cavern on Anguilla. Both of these studies were conducted by the authors. A general similarity also can be noted between the Harney site ceramics and Amerindian samples from the Lesser Antilles (e.g., Bullen and Bullen, 1972:130–131, 142; Gauthier, 1974; Goodwin, 1979:238–244). In fact, it would be difficult to differentiate the Harney site ceramics from Amerindian ceramics on the basis of temper attributes alone. However, these ceramics can be differentiated from local Amerindian ceramics on the basis of other distinctive attributes. It seems very likely that the Afro-Montserratian ceramics from the Harney site were manufactured on Montserrat on the basis of temper constituents which are available in geological deposits of volcanic origin (Rea, 1974; Watters, 1980).

Texture.—As might be expected from the high proportion of temper in each case, the textural attributes for the eight vessels reveal a ceramic paste of medium body for all vessels except two (Table 2; Fig. 6, 7A, 7B, 9A, and 9B). The two exceptions, vessels 1 and 5 (Fig. 6A, 6C, 8A) are similar to the others, but exhibit a more fine bodied paste. Most vessels likewise exhibit some extrusive temper, but it is relatively uncommon and did not typically produce fine surface fractures. Blocky angular fractures with some internal laminations characterize all broken edges of the ceramics and vesicles are discernible in at least five vessels. While the laminations and vesicles are indicative of incomplete kneading of the paste (cf. Rye 1981:39–40, Fig. 23), the other textural attributes reflect the generally thorough degree of consolidation employed in the forming of these vessels.

Other Black-made and presumed Black-made samples exhibit generally similar textural attributes (e.g., Armstrong, in press; Bullen and Bullen, 1972:148; Ferguson, 1980; Gartley, 1979). In all these samples, the ceramic paste is relatively coarse earthenware and obviously distinct from European earthenwares (e.g., Deagan, 1987:35–47).

Manufacture.—Coiling was employed to manufacture seven of the vessels. Although only slightly evident on the basis of coil fractures, coils were discernible through careful examination of sherd cross-sections (Fig. 6B, 6F, 7A, 9A, and 9B). Mean coil heights and thicknesses for each vessel range from 9.65 mm to 12.15 mm and 6.53 mm to 10.05 mm, respectively, with an overall mean height of 10.88 mm and mean thickness of 7.22 mm for the entire sample. The mode of construction remains unknown for vessel 3.

Some Black-made pottery in the West Indies has been wheel-thrown (and kiln-fired) on the basis of available historic documentation that suggests development from European traditions (e.g., Handler, 1963*a*, 1963*b*; Handler and Lange, 1978:139–140). Coiled and other nonwheel techniques are traditional African modes of construction (Armstrong, in press), which have survived in the West Indies on Antigua and Nevis (e.g., Handler, 1964; Handler and Lange, 1978:140). Of par-

ticular interest, the three specimens noted above from the Newton cemetery on Barbados were certainly manufactured using a coiling technique on the basis of personal examination. Likewise, Afro-Jamaican specimens from the Drax Hall plantation on Jamaica typically exhibit coil construction (Armstrong, in press). All or nearly all Amerindian ceramics from the West Indies exhibit coil construction as well (e.g., Bullen and Bullen, 1972:142; Rouse, 1939:46), and so, this attribute only serves to differentiate the Harney specimens from wheel-thrown ceramics made in a European tradition and does not differentiate them from Amerindian specimens.

Surface finish.—The entire sample is characterized by smoothing to one degree or another (Table 2). Most of the vessels have smooth interior, lip, and exterior surfaces (Fig. 4, 5, 7–9). The most notable exceptions include the exterior surface of vessel 4 and the interior surface of vessel 7, which exhibit smooth irregular surfaces that were not finished to the same degree as the other surfaces on the same vessel or the other vessels in this sample. The uniform smooth surfaces often reveal evidence of smoothing done with a soft yielding tool on the basis of subtle, fine parallel striations (cf. Shepard, 1965:190, Fig. 13F). No slips, burnishing or other more elaborate modes of surface finish are represented on the Harney ceramics, a fact which differentiates them from even the least elaborate Amerindian ceramics from local contexts in the Lesser Antilles (e.g., Hoffman, 1979). It should be noted that these vessels better match other Black-made samples in terms of surface finish (e.g., Armstrong, in press; Bullen and Bullen, 1972:148; Ferguson, 1980; Gartley, 1979; Wheaton and Garrow, 1985).

Vessel morphology.—Few morphological attributes can be specified for this small and fragmentary sample (Table 3). Three vessels have preserved rims, however, and among them include examples of three different lip forms and two different rim shapes. The lip forms include a rounded form on vessel 1, a square form on vessel 8 and an intermediate square-round form on vessel 5. Vessels 1 and 5 exhibit apparent straight rims, while vessel 8 exhibits an incurvate rim (Fig. 10). All of the entire sample of eight vessels were cylindrical in overall form and it seems obvious that at least vessels 1, 5 and 8 were cylindrical jars, or less likely bowls on the basis of these limited morphological attributes and their preserved thicknesses. Vessel 4 also likely represents a jar of some sort on the basis of its preserved curvature. Possible analogues to these vessels are present in other Black-made samples where bowl and "olla" jar forms predominate (e.g., Armstrong, in press; Bullen and Bullen, 1972:148–149; Deetz, 1977:147; Ferguson, 1980; Gartley, 1979:47–48, Fig. 1, 2; Moran et al., 1982:92; Nicholson, 1983, 1985; Wheaton and Garrow, 1985, fig. 11.6). A broader range of vessel forms is known from Amerindian samples in the West Indies, including comparable but distinctive jar forms (e.g., Bullen and Bullen, 1972; Rouse, 1939).

Metrics.—Relatively few measurements are available to allow characterization of the Harney ceramics, but the available measurements do document the relatively thick nature of the preserved sherds (Table 3). Lip thickness maximally ranges from 8.85 mm to 10.10 mm within a vessel and from 8.15 mm to 10.10 mm between vessels, with a sample mean of 8.84 mm ($N = 3$). Thickness at 1 cm below the lip maximally ranges from 10.00 mm to 10.85 mm within a vessel to 9.40 mm to 10.85 mm between vessels, with a sample mean of 9.89 mm ($N = 3$). Neck thickness maximally ranges from 8.20 mm to 9.40 mm within a vessel and from 8.20 mm to 9.05 mm between vessels, with a sample mean of 8.93 mm ($N = 2$).

Body thickness is better represented than other available measurements. It

Table 3.—Harney site Afro-Montserratian ceramic vessel attributes. Munsell color designation key listed below.

Vessel designation Number of specimens	1 (8)	2 (1)	3 (1)	4 (3)	5 (3)	6 (2)	7 (1)	8 (1)
Morphology								
Square lip	X							X
Round lip								
Square/round lip		X	X	X	X	X	X	X
Unknown lip								
Incurvate rim								
Straight rim	X				X			
Unknown rim		X	X	X		X	X	
Metrics (mm)								
Lip	8.15	—	—	—	8.15–10.10	—	—	8.45–9.20
1 cm below lip	9.40	—	—	—	9.65–10.00	—	—	10.00–10.85
Neck	8.20–9.40	—	—	—	9.05	—	—	—
Body	5.65–8.00	6.20–6.75	9.15–9.55	4.55–6.85 7.80–10.10	—	7.40–7.90	6.40–8.45	—
Base	—	—	—	—	—	—	—	—
Oral diameter	240	—	—	—	160	—	—	240
Color (see below)								
Exterior	97/137	137	107	127/107	76	92/137	137	66
Interior	101/107	134	101	129/132	106/137	122/132	134	62
Core	132	137	105	138	137	132	137	126
Firing								
Oxidized environment				X				X
Reduced environment	X	X	X		X	X	X	
Fast cooling	X	X		X	X	X	X	X
Slow cooling			X					
Decoration								
None observed	X	X	X	X		X	X	X
Incision					X			
62—reddish yellow (5YR 6/6)			105—dark brown (7.5YR 3/2)			129—yellowish brown (10YR 5/4)		
66—reddish brown (5YR 5/3)			106—dark brown (7.5YR 3/4)			132—dark gray (10YR 4/1)		
76—dark reddish brown (5YR 3/2)			107—black (7.5YR 2/0)			134—brown/dark brown (10YR 4/3)		
92—light brown (7.5YR 6/4)			122—pale brown (10YR 6/3)			137—very dark gray (10YR 3/1)		
97—brown (7.5YR 5/4)			126—gray (10YR 5/1)			138—very dark grayish brown (10YR 3/2)		
101—brown/dark brown (7.5YR 4/2)			127—grayish brown (10YR 5/2)					

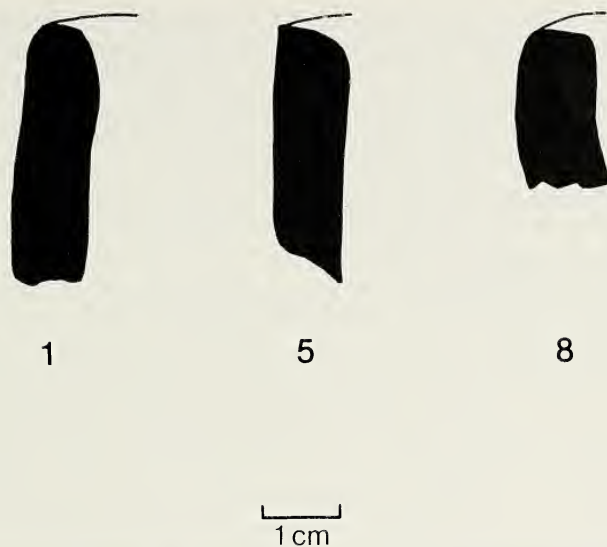


Fig. 10.—Rim profiles for Harney site vessels. Numbers 1, 5, 8 correspond to vessel designations.

varies from 5.65 mm to 8.00 mm within a vessel and from 4.55 mm to 9.55 mm between vessels, with a sample mean of 7.26 mm ($N = 6$). Apparent basal measurement ranges from 7.80 mm to 10.10 mm within a single vessel and oral diameter ranges from 160 mm to 240 mm between vessels, with a sample mean of 213 mm ($N = 3$) for oral diameter.

Although few precise metrics are available for other similar ceramics, the Harney sample generally matches the size and thickness of other comparable samples including the Newton cemetery sample (e.g., Bullen and Bullen, 1972:148; Gartley, 1979:47–48; Wheaton and Garrow, 1985: table 11.1). In fact, the range in oral diameters in a sample from St. Croix, 150 mm to 250 mm, almost precisely matches the range in oral diameters for the Harney ceramic vessels, which, as noted above, is 160 mm to 240 mm (Gartley, 1979:47–48). In general, Amerindian ceramics are inclusive of the size and thickness range of the Harney sample, but some Amerindian specimens are certainly thinner than the Harney specimens.

Color and firing attributes.—The color attributes are the result of firing conditions, clay sources, and conditions of usage, or discard and post-depositional alteration (Table 3).

Exterior colors are overall quite dark and variable, ranging from dark reddish brown (5YR 3/2) to very dark gray (10YR 3/1) and black (7.5YR 2/0) on firing clouds (Fig. 9A). On one “atypical” vessel (vessel 8) the exterior color is reddish brown (5YR 5/3). The interior colors are similarly dark, although the range is slightly different. Pale brown (10YR 6/3) to brown/dark (7.5YR 4/2 and 10YR 4/3) and black (7.5YR 2/0) characterize the interior colors. The one atypical vessel has a reddish yellow interior color (5YR 6/6). These variable surficial colors indicate reduced firing in controlled nonkiln environments for all vessels except atypical vessel 8, which was fired in an oxidized environment.

Core colors as seen in fresh cross-sections of each vessel are typically some variety of gray (10YR 5/1) to very dark gray (10YR 3/1). The sharply graded colors from exterior and interior surfaces to the cores indicate fast cooling for all vessels and it seems that carbon-rich clays were employed in each case.

The near uniformity of the reduced firing environments differentiates the Harney vessels from Amerindian samples from local Antillean contexts, which seem to have been more typically fired in oxidized environments. However, the available data for other Black-made samples suggests that these share very similar characteristics of firing in open hearth, nonkiln environments with the Harney vessels (e.g., Armstrong, in press; Bullen and Bullen, 1972:148; Ferguson, 1980; Gartley, 1979; Wheaton and Garrow, 1985: table 11.1). Of note, the Newton cemetery specimens share dark cores with the Harney specimens, but seem to have been fired in oxidized environments.

Decorations.—A near absence of original and/or preserved decoration is a notable characteristic of the Harney ceramics (Table 3). The one exception, vessel 5, has incised decoration on the rim and neck/shoulder portions of the vessel (Fig. 8B). A single incomplete incision is preserved on the rim and another segment of an incision is present on the neck/shoulder portion. The example on the rim extends from 14.60 mm below the lip to some undetermined distance below the rim. As preserved, the incisions vary from 1.90 mm to 2.70 mm in width, depending on the degree of oblique tipping in their application, and both exhibit a rounded cross-section. The oblique tipping of the incisor created elements which in some ways resemble punctations.

Decoration does not seem to have been emphasized by the potters who made the Afro-Montserratian ceramics found at the Harney site, which provides a notable contrast to most, but not all of the Amerindian ceramics from local and regional contexts (e.g., Bullen and Bullen, 1972; Goodwin, 1979; Hoffman, 1979; Rouse, 1939). Although most other known Black-made samples from the Antilles and elsewhere are undecorated (e.g., Armstrong, in press; Bullen and Bullen, 1972; Gartley, 1979; Nicholson, 1983; Wheaton and Garrow, 1985: table 11.1), incision is a traditional type of decoration, among others in West African ceramic traditions (Ferguson, 1980:19).

INTERNAL CORRELATIONS

Consideration of the nature and distribution of the Afro-Montserratian ceramics from the Harney site is obviously hampered by the small size of the sample and the conditions of the salvage excavation which was, by necessity, incomplete. As noted above, the distribution of the ten sherds (representing three vessels) recovered in situ reveals that these specimens were not likely intentional grave goods, but, rather, represent incidental inclusions of already broken ceramic vessels. This interpretation is substantiated by the fact that portions of vessel 1 were recovered from in situ burials 1 and 3. Moreover, the small size of the sherds, little or no evidence of modern breakage, and the small number of specimens attributable to any one vessel from either in situ or disturbed contexts all seem to substantiate the interpretation that the vessels were broken across the site some time prior to interment of the human burials. If the ceramics had been intentionally interred as grave goods, it seems likely that more complete specimens would have been chosen and these would have been more completely represented in the available sample even under conditions of differential disturbance and subsequent excavation of the 17 burials. This does not resolve the issue of the immediate origin of these fragmentary ceramics, however; that is, how they came to be utilized and/or discarded on the Harney site. Following an intriguing discussion by Handler and Lange (1978:138–139), it does seem possible that the Afro-Montserratian ceramics may represent fragments of containers “used in burial or postinterment

activities,” or that they “reflect the remains of food or drink vessels that were carried by workers in adjacent fields.” This issue simply cannot be resolved on the basis of available information.

The issue of sample consistency is also an important consideration. With the exception of vessel 8, the fragmentary vessels seem to be closely related to one another. In point of fact, vessel 8 can be differentiated only on the basis of its surficial colors and possibly its rim form. Attributes of temper constituents, temper proportions, texture, surface finish, mode of manufacture and lack of decoration establish a general similarity to the balance of the sample. It seems likely that vessel 8 was manufactured by the same potters, or closely related potters, who then subjected it to an oxidizing rather than a reducing firing environment. Of course, it is also possible that vessel 8 represents a Black-made import from another Antillean island, such as Nevis where similar reddish colored ceramics have been made into the 20th century (Handler, 1964).

The attribution of the Harney ceramics to Black potters who worked locally has been variably addressed in different portions of this analysis. Although the nature of the temper constituents allows suggestion that these vessels were made locally and as such superficially resemble local Amerindian ceramics, the differences between the Harney ceramics and Amerindian ceramics are emphasized in consideration of the attributes of surface finish, firing and some aspects of texture, morphology, metrics and decoration. Thus, it seems prudent to argue that, although the Harney colonoware ceramics were not products of Amerindian potters, they were made locally, most likely on Montserrat. We have assigned the Harney Afro-Montserratian ceramics to Black potters because of their general similarity to other known examples of Black-made ceramics from contexts in the West Indies and elsewhere.

EXTERNAL CORRELATIONS

Comparison of the Harney site Afro-Montserratian ceramics with other similar samples is hampered by the relatively little attention that these materials have received in archaeological studies in the West Indies and elsewhere. In point of fact, it has been only a decade or two since the distinctive nature of Black-made ceramics was first recognized in archaeological analyses. Many details about these ceramics remain to be elucidated, especially since there is little known historical documentation available for these hand-built, open hearth-fired vessels. Handler and Lange (1978:139–144) have documented that earthenware ceramics were manufactured by Black slave potters on Barbados as early as the latter half of the 17th century. As reported in early sources, these ceramics were manufactured by males using a wheel and kiln technology derived from Europe. However, more traditional African hand-built coil manufacture and open hearth firing was apparently practiced as well, most likely by men and women (Handler, 1963*b*; Handler and Lange, 1978:140). It is this latter tradition, which is more African than European or Amerindian in origin, that is represented by the Harney ceramic sample. We have chosen to label this tradition as Afro-Montserratian to distinguish it from other Black-made ceramics.

In any case, Black-made ceramics seem recognizable on many different islands in the West Indies, but few comparative data have been reported for most samples. Such ceramics are apparently well documented on Jamaica by Armstrong (in press) and Matthewson (cited in Gartley, 1979, and Handler and Lange, 1978) and a variety of smaller islands, including Antigua, St. Croix, St. Thomas, St.

John, St. Kitts, St. Martin, and St. Vincent, among others (Bullen and Bullen, 1972; Gartley, 1979; Nicholson, 1983). In most, if not all cases, ceramics that can be labeled as Black-made have been derived from archaeological contexts that are *minimally* dated to the latter half of the 18th century and the first half of the 19th century (e.g., Armstrong, in press; Deetz, 1977; Gartley, 1979; Handler and Lange, 1978; Moran et al., 1982; Wheaton and Garrow, 1985).

Although well represented on some of these islands, similar Black-made ceramics do not seem well represented on Barbados, at least not in the samples available to Handler and Lange (1978:141–144). Handler and Lange go on to consider what sort of geographical, ecological and historical factors may have fostered or hindered the continuation of an African-based tradition or traditions in these contexts and they demonstrate the utility of ceramics as a cultural indicator. It seems likely that additional analyses of African ceramic samples from the West Indies and elsewhere will shed light on some of these intriguing questions.

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LATE WISCONSINAN APPALACHIAN HERPETOFAUNAS:
RELATIVE STABILITY IN THE MIDST OF CHANGELESLIE P. FAY¹

ABSTRACT

Fossil herptiles from eastern North America exhibit less dramatic Wisconsinan-Holocene range adjustments than many contemporaneous mammals, birds, and plants. Mammal and bird faunal lists consist of current residents of the fossil locality plus a sizeable component of taxa that ranges to the north or west. Herptile lists include area residents with a few forms now removed to the south. Factors responsible for the varying responses to climatic change between and within vertebrate classes have not yet been adequately addressed. Most Late Wisconsinan Appalachian herpetofaunas neither support nor contradict the climatic equilibrium hypothesis, because herptiles are either insensitive to climatic and biotic change or an appropriate transfer function has not been formulated to provide a partial climatic analog. Although range limits of many plants and animals changed by hundreds of kilometers in response to the late glacial-interglacial climatic shift, herptiles in eastern North America seem to have been less strongly affected by these events. Previously reported extralimital records of *Masticophis flagellum*, *Crotalus adamanteus* (Natural Chimneys, Virginia), and *Bufo americanus copei* (New Paris No. 4, Pennsylvania) are rejected.

INTRODUCTION

Until the last twenty years, environmental reconstructions developed from fossil evidence depended on the assumption that current (i.e. before human disturbance) patterns of plant communities existed through most of the Quaternary Period. With allowances for areas covered by glacial ice and perhaps a severe "periglacial" fringe, the modern communities were mapped as if they migrated intact north and south in response to glacial-interglacial cycles (cliseral shift model; Brunnschweiler, 1962; Dansereau, 1957; Dillon, 1956; Flint, 1971; Martin, 1958). The boundaries of these dislocated communities were delineated on scanty pollen evidence with no radiometric time frame and were fortified by individual large vertebrate discoveries. As data points were few and non-uniformly spaced, much of this early reconstruction was based on inference. Animals now associated with each community were assumed to have moved along with the plants (Martin, 1958).

The use of screen-washing techniques for recovering smaller macroscopic fossils (Hibbard, 1949; McKenna, 1962) has made it possible to utilize small animals in paleoenvironmental reconstructions. Small animals are often more closely linked to microhabitat than are large forms and less likely to migrate long distances through anomalous habitats. Careful stratigraphic documentation makes it feasible to distinguish synchronously deposited and heterochronic fossil accumulations when each contains species not now sympatric.

The distribution of many small animals was markedly altered by glacial advances and retreats. Discovery and analysis of many local faunas and pollen profiles has demonstrated that these changes in distribution did not occur as entire community (cliseral) shifts, but as responses by individual species of plants (e.g.,

¹ San Bernardino County Museum, Redlands, CA 92374.
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Davis, 1976) and animals (e.g. Graham, 1985) according to tolerance limits and interactions during climate-driven dissolution and reformation of communities (Graham and Lundelius, 1984).

The new interpretation of Quaternary environmental response is based mainly on information from the pollen and mammal fossil record. Comparatively little information has been reported on fossil herptiles (reptiles and amphibians), although they have been noted in eastern North American Quaternary local faunas for almost 90 years (e.g. Cope, 1899). Herptiles were simply listed in many papers with little or no interpretation and evaluation. Previous reviews of Quaternary climatic effects on herptiles relied almost solely on evidence from present distribution and speciation (i.e., morphologic differentiation between living taxa) (Aufenberg and Milstead, 1965; Blair, 1965; Schmidt, 1938; Smith, 1957). Twenty years ago, the fossil record was as yet so poorly known that "... the best we can hope for is to determine the relation to present distribution and present evidence of speciation to major shifts in climatic conditions" (Blair, 1965:543). Fortunately, the fossil record has since provided a number of herpetofaunas that can be used to study climatic conditions more directly. The suitability of fossil herptiles as climatic proxies (Bryson, 1985) has not been thoroughly evaluated. Although this study indicates they may not serve well as paleoclimatic indicators, further examination of modern herptile ecology in regard to the fossil record will be necessary to determine if a transfer function (Bryson, 1985) can be formulated.

Herpetofaunas from Frankstown Cave, New Paris No. 4, Natural Chimneys, Clark's Cave, Baker Bluff Cave, and Kingston Saltpeter Cave (Fig. 1) were chosen for this study because their relatively high species diversity suggested the potential for meaningful comparison with co-occurring mammals and birds previously reported. In prior studies, the finding of temperate and even supposedly austro-riparian herptiles in several of these local faunas contradicted the presence of boreal mammal and bird taxa. This apparent anomaly implies either: (1) The herptiles "leaked" into the deposits after the boreal + temperate mammal and bird accumulations, resulting in a heterochronic assemblage. Two corollaries are (i) no herptiles were present when the mammals and birds accumulated, or (ii) herptiles were present but did not fossilize (Fay, 1986). (2) The anomaly shows that herptiles responded differently to climatic change than did the more boreal mammal and bird taxa.

Two main objectives of this study are to (1) document regional relationships among central and southern Appalachian herptiles at the close of the most recent glaciation, and (2) compare inferred climatic effects on the herptiles with previously interpreted effects on mammals and birds.

PROCEDURES

All materials except that from Kingston Saltpeter Cave were collected by field parties directed by the Section of Vertebrate Fossils, The Carnegie Museum of Natural History, and are housed at that institution. Kingston specimens were collected by the Kingston Saltpeter Cave Study Group, Clayton County Cavers, National Speleological Society Grotto No. 285, and are repositied at Berry College, Rome, Georgia. Details of field sampling procedures can be found in the primary references for each locality cited in the Annotated Faunal Lists. Modern skeletal specimens of the Herpetology and Ichthyology Division, Michigan State University Museum, were used for comparative study of the fossils.

Explanations of identification methods are provided in the Selected Systematic Accounts for new or modified techniques. Both qualitative and quantitative morphometric methods were employed for identifying the fossils, because each is not entirely reliable alone. Taxonomy above the generic level follows Dowling and Duellman (1978). Genera, species, common names, and geographic distributions are after Conant (1975), Martof et al. (1980), and McCoy (1982).

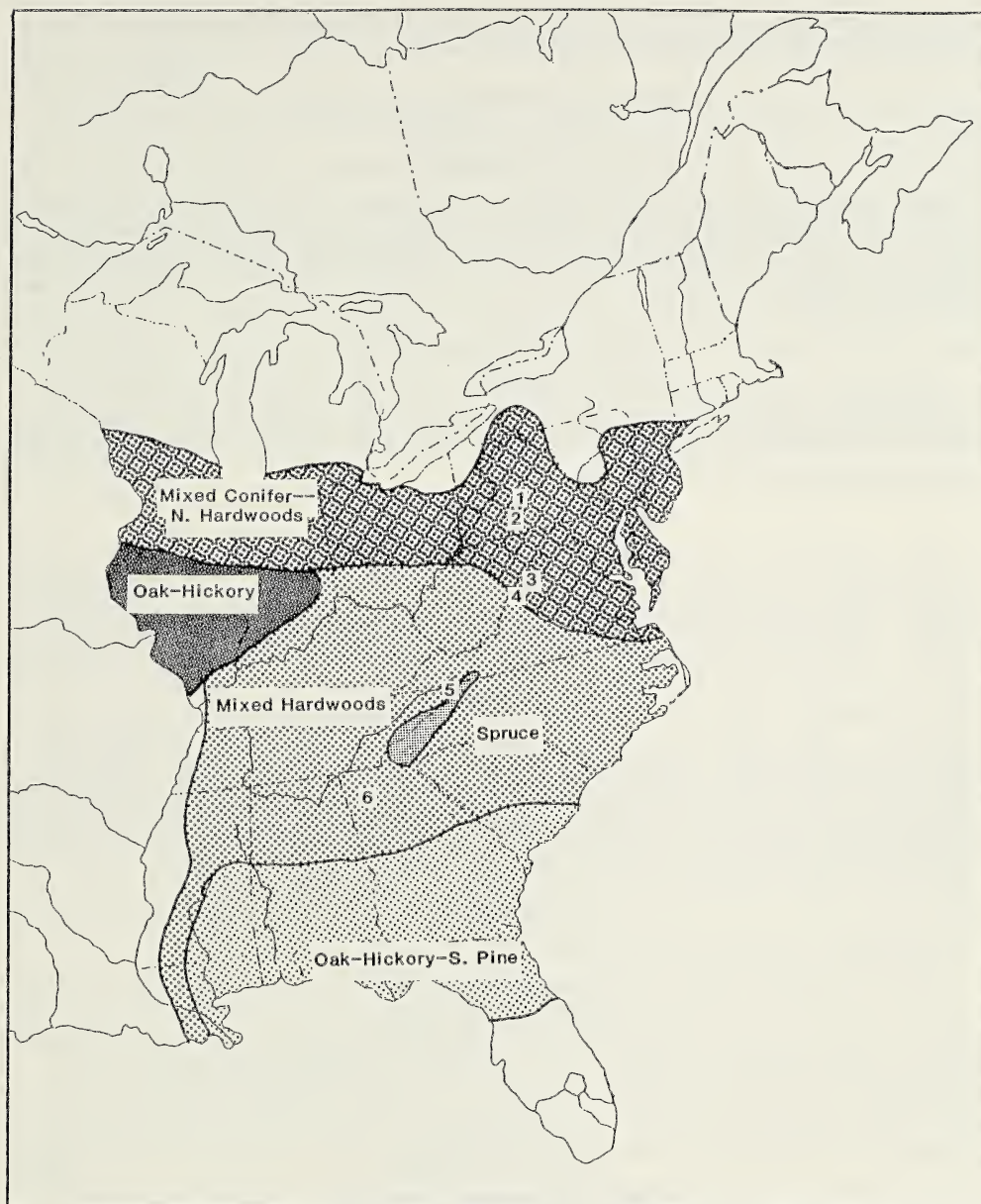


Fig. 1.—Location of six Late Wisconsin-early Holocene local faunas in the central and southern Appalachian region. Base map illustrates selected paleovegetation units of 10,000 yr BP (after Delcourt and Delcourt; 1981:149, Fig. 7). 1—Frankstown Cave, PA; 2—New Paris Sinkhole No. 4, PA; 3—Natural Chimneys, VA; 4—Clark's Cave, VA; 5—Baker Bluff Cave, TN; 6—Kingston Saltpeter Cave, GA.

ABBREVIATIONS

BB—Baker Bluff Cave, CC—Clark's Cave, CL—centrum length, FC—Frankstown Cave, KSC—Kingston Saltpeter Cave, NAW—neural arch width, NC—Natural Chimneys, NP4—New Paris No. 4, NSH—neural spine height, NSL—

neural spine length, POPR—postzygopophysis to prezygopophysis length, PRPR—prezygopophysis width, ZW—zygosphen width.

SELECTED SYSTEMATIC ACCOUNTS

Class Amphibia Family Plethodontidae

Many plethodontid taxa are difficult to distinguish when alive and may well prove impossible to separate as disarticulated fossils. Trunk vertebrae of the two subfamilies and several plethodontine genera and species may be identified with relative certainty.

Subfamily Desmognathinae

Occurrence.—NP4, NC, CC, BB, KSC.

The dusky salamanders occasionally have been elevated to family rank on the basis of characteristic opisthocelous vertebrae (Soler, 1950). Attempts at specific determinations have not been successful.

Subfamily Plethodontinae

This subfamily includes all non-desmognathine plethodontids. Two genera, *Gyrinophilus* and *Pseudotriton*, have distinctive “false opisthocelous” vertebrae (Soler, 1950:463). The remaining eastern North American plethodontines have not previously been thoroughly examined for distinctive osteological morphology that would allow identification of disarticulated fossils to the species level. Size and geographic range have been used for identifications (e.g., Holman, 1967; Lundelius, 1967; Richmond, 1964; Richmond in Guilday et al., 1964) but, as with desmognathines, a great deal of overlap exists between taxa. Members of the genus *Eurycea* may be distinguished by the characters listed below, and the remaining plethodontines are informally grouped as “*Plethodon*-type,” including *Aneides*, *Hemidactylium*, and *Plethodon* in the region of this study.

Eurycea sp.

Occurrence.—NP4, NC, CC, KSC.

Eurycea vertebrae may be distinguished by a tendency toward the false opisthocelous condition, well-separated transverse processes, condyle situated ventrally on the centrum, and with neural spine extending almost full length of the centrum. Species determination of fossil vertebrae has not yet been attempted.

Order Anura

Family Bufonidae *Bufo americanus* Holbrook

Occurrence.—FC, NP4, NC, CC, BB, KSC.

B. americanus ilia may be distinguished by the broad base of the ilial prominence in lateral view (Holman, 1967). The dorsal protuberance is oriented anterodistally in mature *B. americanus*, but perpendicular to the longitudinal axis of the ilial shaft in other eastern North American *Bufo*. *B. americanus* ilia that exceed the modern size range for the species have been reported from Ladds Quarry, Georgia (ilial acetabular height 16.5 mm; Holman, 1967:157, Table 1). Kingston Saltpeter Cave, located about 13 km from Ladds, yielded the largest ilium in this study with acetabular height 8.8 mm. *Bufo americanus* osteology is extremely variable

in the morphological details relied upon for fossil identifications and a comprehensive examination of both modern and fossil specimens throughout the distribution is needed.

Bufo americanus copei was identified by Richmond (in Guilday et al., 1964) from New Paris No. 4. The subspecific determination was based on small size and association with boreal mammals. I have repeated this listing with strong reservation because of the need for morphological study already mentioned. Another small subspecies, *B. a. charlesmithi*, also exists, although in the southwest portion of the species range, rather than the northern fringe, where *B. a. copei* occurs (Conant, 1975:404, Map 261). Size and co-occurrence with extralimital mammals are insufficient criteria for subspecific identification of fossils. Cook (1984) does not support subspecific status for *B. a. copei* because of the wide zone of intergrading characters with the nominate subspecies.

The New Paris fossil ilia likely represent small, but mature *B. a. americanus*, the zoogeographic implications of which would accord with the rest of the herpetofauna.

Family Hylidae

Hyla chrysoscelis/versicolor

Occurrence.—FC.

Grey treefrogs are distinguished by call rates and chromosome counts, but no osteological criteria have been delineated that separate the two species.

Hyla crucifer (Wied)

Occurrence.—FC, NP4, CC, KSC.

The New Paris *H. crucifer* represent individuals larger than known modern specimens in snout-vent length by 5 mm (Lynch, 1966). Irvingtonian *H. crucifer* from Cumberland Cave, Maryland (Lynch, 1966) and all other specimens of this study are within modern size range. The paleoenvironmental significance of clinal variability for many Appalachian herptiles requires additional study. *Hyla* previously reported from Natural Chimneys and Baker Bluff Cave (one ilium each) have been re-identified as *Scaphiopus holbrooki* and juvenile *Bufo* sp., respectively.

Family Ranidae

Rana pipiens-group

Occurrence.—FC, NP4, NC, CC, KSC.

No method has been devised that adequately separates ilia of the leopard frog complex (Holman, 1977a). This group includes at least four parapatric species in eastern North America, distinguished by soft anatomy and call rates (Conant, 1975).

Class Reptilia

Order Testudines

Family Emydidae

?*Clemmys insculpta* (Le Conte) or

?*Pseudemys concinna* (Le Conte)

Occurrence.—KSC.

A badly eroded proximal left humerus resembles both *C. insculpta* and *P. concinna* in size and gross morphology but is not distinguishable. Both turtles are present in the Ladds Quarry local fauna (Holman, 1967, 1985a). If the specimen

is indeed a *C. insculpta* humerus, it is the only extralimital herptile occurrence at Kingston Saltpeter Cave.

Order Squamata
Suborder Serpentes

Snake vertebrae present an intricate and often frustrating exercise in identification. A large comparative collection is necessary, for the vertebrae are not only morphologically diverse, but variable among and within taxa and individuals.

Only mid-trunk vertebrae were used for identification in this study because adequate criteria are unknown for identifying anterior trunk and caudal vertebrae. Guidelines offered by Holman (1981) were used to separate subfamily groups. Calculation of vertebral mensural ratios, pioneered by Auffenberg (1963) and expanded by Meylan (1982) was utilized along with qualitative characters.

Family Colubridae
Subfamily Natricinae

This subfamily may be divided on the basis of vertebral size. *Seminatrix*, *Storeria*, *Tropidoclonion*, and *Virginia* vertebrae are less than 3 mm CL. Larger natricine vertebrae can be separated according to length-width ratios. *Thamnophis* vertebrae have CL/NAW ratios greater than 1.75. For *Clonophis*, *Nerodia*, and *Regina*, this ratio is less than or equal to 1.5.

?Regina septemvittata (Say)

Occurrence.—NP4, NC, CC.

Most members of the genus *Regina* have vertebral characters intermediate between my "small" and "large" natricine forms. According to these criteria of vertebral ratios and morphologic characters, *R. septemvittata* closely resembles the genus *Thamnophis*, except that the former has more abbreviated neural spines (Auffenberg, 1963) and blunter accessory processes. It is otherwise difficult to separate these two taxa.

Storeria dekayi (Holbrook)

Occurrence.—NP4, NC, CC, KSC.

Storeria occipitomaculata (Storer)

Occurrence.—NP4, NC, CC.

Storeria may be confused with *Virginia*. *Storeria* has NSL/ZW ratios averaging greater than 1.10, *Virginia* less than 1.05 (Auffenberg, 1963:192, table 21). *S. dekayi* can be very difficult to distinguish from *S. occipitomaculata*. Three ratios in combination have proven useful (*S. occipitomaculata* values in parentheses): POPR/CL > 1.08 (<1.07); NSL/ZW < 1.17 (>1.17); CL/NAW < 1.91 (>1.94).

Thamnophis brachystoma (Cope)

Occurrence.—FC.

T. brachystoma vertebrae are distinguished from other small (<5 mm CL) natricines by taller neural spines, CL/NAW of 1.55–1.75, and POPR/PRPR of 1.00 to 1.03.

Virginia striatula (Linné)

Occurrence.—NC, CC, KSC.

Virginia valeriae Baird et Girard

Occurrence.—FC, NP4, NC, CC, KSC.

Vertebral ratios serve to distinguish the two *Virginia* species (*V. valeriae* values in parentheses): POPR/NAW > 2.00 (<1.75); CL/NAW > 1.77 (<1.55); NSL/ZW > 0.97 (<0.74).

Subfamily Colubrinae
Coluber or *Masticophis*

Occurrence.—NP4, NC, CC, BB, KSC.

I have discovered no reliable criteria to separate vertebrae of *Coluber* and *Masticophis*, although Meylan (1982) has had some success. Holman's (1981) cautionary note regarding *M. flagellum* determinations where sympatric with *Coluber* or other *Masticophis* is heeded. Until distinguishing features are discerned, I prefer to assign large colubrine vertebrae to "*Coluber* or *Masticophis*." For this reason, I reject Richmond's determination of *M. flagellum* (in Guilday, 1962) for Natural Chimneys material.

Subfamily Lampropeltinae
Elaphe guttata (Linné)

Occurrence.—NP4, NC, CC, KSC.

Elaphe obsoleta (Say)

Occurrence.—NP4, NC, CC, KSC.

Auffenberg (1963:181, fig. 29) separated vertebrae of *E. obsoleta* from *E. guttata* by NSH/NSL ratio *versus* CL. Meylan (1982:33, table 6) achieved about 90% accuracy separating the two species by means of four length/width ratios. Also, in anterior view, the accessory processes of *E. obsoleta* are laterally directed, while those of *E. guttata* are slightly dorsolaterally directed.

Lampropeltis calligaster (Harlan)

Occurrence.—NP4, CC, KSC.

Lampropeltis getulus (Linné)

Occurrence.—NP4, NC, CC, BB, KSC.

Lampropeltis triangulum (Lacépède)

Occurrence.—NP4, NC, CC, BB, KSC.

L. calligaster may be separated from *L. triangulum* by the distinctly lower neural spines and anteriolateral direction of the accessory processes in the latter. *L. getulus* has the most strongly developed subcentral ridges among lampropeltines (Auffenberg, 1963). It most closely resembles *L. calligaster*, which has a haemal keel that does not widen toward the condyle as in *L. getulus* (Auffenberg, 1963). *L. getulus* also has shorter vertebrae with more pronounced dorsoventral flattening of the accessory processes than in *L. calligaster*.

Lampropeltinae, indeterminate

Occurrence.—FC.

Richmond (1964) tentatively assigned nine juvenile vertebrae to *L. triangulum*. I do not consider it prudent to assign such young specimens to species although they are certainly lampropeltines.

Table 1.—Checklist of herptiles from six late Wisconsinan–early Holocene Appalachian local faunas.

Taxon	Locality					
	FC	NP4	NC	CC	BB	KSC
<i>Cryptobranchus alleganiensis</i>					X	
<i>Necturus maculosus</i>					X	
<i>Notophthalmus viridescens</i>	X	X	X	X		X
<i>Ambystoma maculatum</i> -group		X	X	X	X	X
<i>Ambystoma opacum</i> -group			X	X	X	X
<i>Ambystoma tigrinum</i>			X			X
<i>Ambystoma</i> sp.	X	X		X	X	
Desmognathinae		X	X	X	X	X
<i>Gyrinophilus porphyriticus</i>			X	X		
<i>Pseudotriton ruber</i>						X
<i>Pseudotriton</i> sp.		X	X	X		
<i>Eurycea</i> sp.		X	X	X		X
<i>Plethodon</i> -type		X	X	X		X
<i>Scaphiopus holbrookii</i>			X	X		X
<i>Bufo americanus</i>	X	X	X	X	X	X
<i>Bufo americanus</i> ? <i>copei</i>		X				
<i>Bufo woodhousei fowleri</i>		X	X	X	X	X
<i>Bufo</i> sp.	X					
<i>Hyla chrysoscelis/versicolor</i>	X					
<i>Hyla crucifer</i>	X	X		X		X
<i>Gastrophyrne carolinensis</i>						X
<i>Rana catesbeiana</i>			X	X		X
<i>Rana clamitans</i>		X	X	X		X
<i>Rana palustris</i>		X	X	X		
<i>Rana pipiens</i> -group	X	X	X	X		X
<i>Rana sylvatica</i>	X	X	X	X	X	
<i>Rana</i> sp.	X					X
<i>Chelydra serpentina</i>			X			
Kinosternidae						X
<i>Chrysemys picta</i>						X
<i>Clemmys insculpta</i>	X					?
<i>Graptemys geographica</i>				X		
<i>Pseudemys</i> sp.						X
<i>Terrapene carolina</i>			X			X
<i>Anolis carolinensis</i>						X
<i>Sceloporus undulatus</i>			X	X		X
<i>Eumeces fasciatus</i>					X	
<i>Eumeces</i> ? <i>laticeps</i>				X		
<i>Scincella lateralis</i>			X			X
<i>Nerodia</i> ? <i>erythrogaster</i>			X			
<i>Nerodia sipedon</i>	X	X	X	X	X	X
<i>Nerodia</i> sp.					X	
? <i>Regina septemvittata</i>		X	X	X		
<i>Storeria dekayi</i>		X	X	X		X
<i>Storeria occipitomaculata</i>		X	X	X		
<i>Storeria</i> sp.						X
<i>Thamnophis brachystoma</i>	X					
<i>Thamnophis</i> ? <i>sauritus</i>		X		X		X
<i>Thamnophis sirtalis</i>	X	X	X	X	X	X
<i>Thamnophis</i> sp.		X	X		X	
<i>Virginia striatula</i>			X	X		X
<i>Virginia valeriae</i>	X	X	X	X		X
<i>Carphophis amoenus</i>	X	X	X	X		X
<i>Diadophis punctatus</i>	X	X	X	X	X	X
<i>Heterodon platyrhinos</i>	X			X	X	
<i>Coluber</i> or <i>Masticophis</i>		X	X	X	X	X

Table 1.—Continued.

Taxon	Locality					
	FC	NP4	NC	CC	BB	KSC
<i>Opheodrys aestivus</i>		X		X		X
<i>Opheodrys vernalis</i>			X	X		
<i>Cemophora coccinea</i>			X	X		
<i>Elaphe guttata</i>		X	X	X		X
<i>Elaphe obsoleta</i>		X	X	X		X
<i>Elaphe</i> sp.					X	
<i>Lampropeltis calligaster</i>		X		X		X
<i>Lampropeltis getulus</i>		X	X	X	X	X
<i>Lampropeltis triangulum</i>		X	X	X	X	X
<i>Pituophis melanoleucus</i>		X				X
<i>Lampropeltinae</i>	X					
<i>Agkistrodon contortrix</i>	X	X	X			X
<i>Crotalus horridus</i>		X	X	X	X	
<i>Crotalinae</i>	X					

Family Viperidae
Subfamily Crotalinae
Agkistrodon contortrix (Linné)

Occurrence.—FC, NP4, NC, KSC.

Crotalus horridus Linné

Occurrence.—NP4, NC, CC, BB.

Large *Agkistrodon* are distinguished from *Crotalus* on the basis of a single fossa in a deep pit along each side of the cotyle in the former (Holman, 1981). A ridge extending from the accessory process ventrolaterally to the parapophysis defines the lateral border of the pit. *Crotalus* vertebrae usually have more than one fossa on a relatively flat surface on either side of the cotyle. Meylan (1982) reported that the number of fossae does not separate all *Agkistrodon* and *Crotalus* vertebrae, because some variation occurs along the vertebral column within individuals.

Richmond's report (in Guilday, 1962) of *C. adamanteus* from Natural Chimneys was based on a large *C. horridus* vertebra. The NSH is well within the range of variation for *C. horridus* and shorter than *C. adamanteus* of comparable size.

ANNOTATED FAUNAL LISTS

Complete specimen lists are available from the author on request. Table 1 permits comparison among herptiles listed for the six herpetofaunas. All identifications are by the author except as noted (¹N. D. Richmond, ²O. A. Peterson, ³H. McGinnis, ⁴J. E. Guilday, ⁵G. H. Van Dam). An asterisk (*) indicates that the taxon no longer occurs near the locality. The designation "sp." is used when fossil and modern distributions indicate more than one member of the genus may be represented in material not assignable to species. Number of specimens is listed in parentheses following catalog number. Repository acronyms are CM—Carnegie Museum of Natural History and BC—Berry College.

Frankstown Cave

Location.—Blair County, Pennsylvania, latitude 40°25'N, longitude 78°22'W.

Accumulation.—Fissure fill.

Fauna.—Peterson (1926) listed six herptiles from Frankstown Cave. Richmond

(1964) restudied the collection and found 12 taxa, including four mis-identifications by Peterson. I have added or re-assigned eight taxa for a new total of 20 fossil herptiles from Frankstown Cave. Plethodontidae, *Storeria*, and *Crotalus* are removed from the list.

Taxonomic changes by the author are as follows: Plethodontidae CM 11149 (1 caudal vertebra) assigned to *Ambystoma* sp., *Bufo* cf. *americanus* CM 11143 (2 ilia) to *Hyla chrysoscelis/versicolor*, *Bufo* cf. *americanus* CM 11143 (1 ilium-juvenile) to *Bufo* sp., *Storeria* sp. CM 11051 (6 trunk vertebrae) to *Virginia valeriae*, *Storeria* sp. CM 11051 (3 trunk vertebrae) to *Thamnophis brachystoma*, *Storeria* sp. CM 11051 (8 trunk vertebrae) to Natricinae indeterminate, *Lampropeltis doliata* CM 11513 (9 trunk vertebrae-juvenile) to Lampropeltinae indeterminate, *Crotalus* sp. CM 11514 (1 trunk vertebra-juvenile) to Crotalinae indeterminate.

<i>Notophthalmus viridescens</i> ¹	CM 11150(8), 11151(2)
<i>Ambystoma</i> sp.	CM 11145(2), 11149(1)
<i>Bufo americanus</i>	CM 11133(3)
<i>Bufo</i> sp.	CM 11134(8)
<i>Hyla chrysoscelis/versicolor</i>	CM 11143(2)
<i>Hyla crucifer</i>	CM 11144(2)
<i>Rana pipiens</i> -group	CM 11147(1)
<i>Rana sylvatica</i>	CM 11140(3)
<i>Rana</i> sp. ²	CM 11136–11139, 11141–11142, 11146, 11317 (38)
<i>Clemmys insculpta</i> ²	CM 11065(2)
<i>Nerodia sipedon</i>	CM 11316(3)
* <i>Thamnophis brachystoma</i>	CM 41871(3)
<i>Thamnophis sirtalis</i> ²	CM 11318(1), 31260(16)
<i>Virginia valeriae</i>	CM 11051(6)
<i>Carphophis amoenus</i>	CM 11351(2)
<i>Diadophis punctatus</i>	CM 11178(1)
<i>Heterodon platyrhinos</i>	CM 31262(1)
<i>Lampropeltinae</i>	CM 11513(9)
<i>Agkistrodon contortrix</i>	CM 11315(2)
Crotalinae	CM 11514(1)

Discussion.—No radiocarbon dates are available from this locality. It is considered of Wisconsinan Age (Kurtén and Anderson, 1980:76–77) and representatives of the eleven extinct mammal taxa reported from Frankstown Cave (Lundelius et al., 1983:333, 337, 338, 339, Table 16.6) are known to have survived elsewhere at least until 12,000 yr BP (Mead and Meltzer, 1984:446, table 19.4).

The additions and changes to the herpetofaunal list represent a 62% increase in taxa reported. This is a disharmonious unit due only to the restricted range of *Thamnophis brachystoma* (Fig. 2), although all members inhabit some portion of the Appalachian Plateau. The extant mammals of the local fauna (61% of mammal taxa) are sympatric in the Valley and Ridge Province in West Virginia and Virginia 100 km south of the locality (Fig. 2). In part because screen-washing recovery techniques were apparently not used at Frankstown (Holland, 1908; Peterson, 1926), this local fauna is not diverse enough to warrant detailed paleoenvironmental reconstruction, but climatic conditions similar to present are indicated by the zoogeographic evidence. No other Late Wisconsinan–early Holocene local

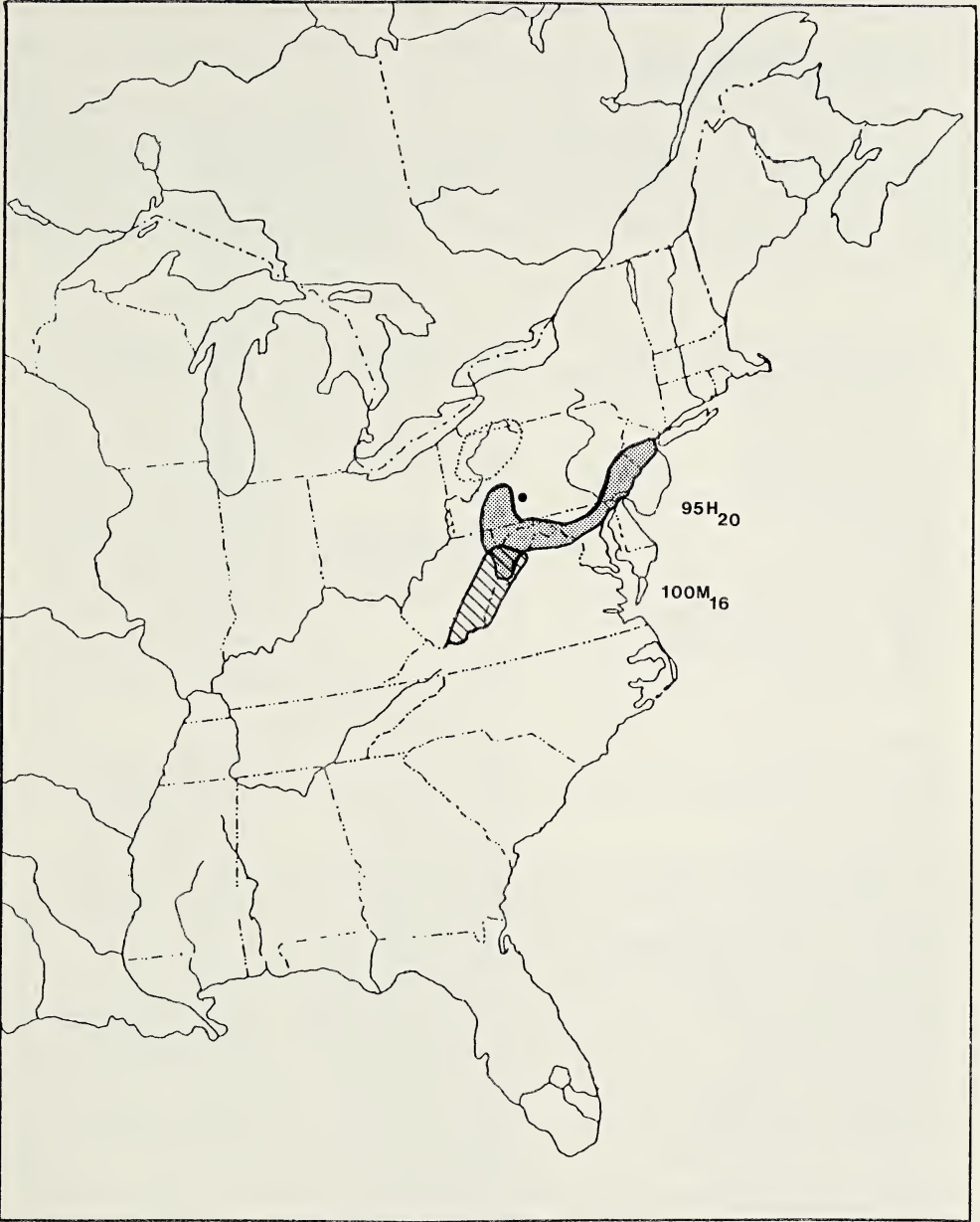


Fig. 2.—Sympatry map for Frankstown Cave local fauna. Dotted line encloses modern range of *Thamnophis brachystoma*. Closed circle indicates fossil locality. Shaded area is herptile sympatry, lined area is mammal sympatry. $95H_{20}$ = 95% of 20 extant herptile phena occur in sympatry area, $100M_{16}$ = 100% of 16 extant mammal phena occur in sympatry.

fauna from the central or southern Appalachian region shares this zoogeographic pattern of near-complete sympatry close to the fossil locality, suggesting that Frankstown Cave local fauna was deposited earlier, perhaps during a Wisconsin interstadial episode.

New Paris No. 4

Location.—Bedford County, Pennsylvania, latitude 40°05'N, longitude 78°39'W.

Accumulation.—Fissure fill.

Fauna.—Richmond (in Guilday et al., 1964) reported 20 fossil herptile taxa from New Paris No. 4. *Regina septemvittata* and *Storeria occipitomaculata* were also identified by Richmond but not included in the published list. I assign *Plethodon* cf. *glutinosus* to *Plethodon*-type. I have identified 14 additional taxa for a total of 34 recognized forms (*B. a. copei* excluded, a subspecific determination that I do not support).

	Unit A	Unit B
<i>Notophthalmus viridescens</i> ¹	CM 41928(11)	CM 41928(9)
<i>Ambystoma maculatum</i> -group (Tihen, 1958)	CM 41929(10)	CM 41929(1)
<i>Ambystoma</i> sp. ¹	CM 41930(11)	CM 41930(1)
Desmognathinae	CM 41931(6)	CM 41931(5)
<i>Pseudotriton</i> sp.	_____	CM 41932(1)
<i>Eurycea</i> sp. ¹	CM 41933(19)	CM 41933(18)
<i>Plethodon</i> -type	CM 41934(203)	CM 41934(137)
<i>Bufo americanus</i> ¹	CM 7950(54)	CM 7952(69)
* <i>Bufo americanus</i> ? <i>copei</i> ¹	_____	CM 7951(12)
<i>Bufo woodhousei fowleri</i>	_____	CM 41935(1)
<i>Hyla crucifer</i> ¹	CM 12513(1), 12534(1)	CM 12533(1)
<i>Rana</i> ? <i>clamitans</i>	CM 41936(3)	_____
<i>Rana</i> ? <i>palustris</i>	CM 41937(1)	CM 41937(2)
<i>Rana pipiens</i> -group ¹	CM 41938(22)	CM 41938(5)
<i>Rana sylvatica</i> ¹	CM 8017(53)	CM 8017(28)
<i>Nerodia sipedon</i> ¹	CM 41939(29)	CM 41939(2)
*? <i>Regina septemvittata</i> ¹	CM 41940(3)	_____
<i>Storeria dekayi</i>	CM 41941(8)	CM 41941(4)
<i>Storeria occipitomaculata</i> ¹	CM 41942(7)	_____
<i>Thamnophis</i> ? <i>sauritus</i>	CM 41943(13)	_____
<i>Thamnophis sirtalis</i> ¹	CM 41944(3044)	CM 41944(2178)
<i>Thamnophis</i> sp.	CM 41945(1898)	CM 41945(167)
<i>Virginia valeriae</i>	CM 41946(23)	CM 41946(2)
<i>Carphophis amoenus</i> ¹	CM 41947(35)	_____
<i>Diadophis punctatus</i> ¹	CM 41948(57)	CM 41948(3)
<i>Coluber</i> or <i>Masticophis</i>	CM 41949(17)	_____
* <i>Opheodrys aestivus</i>	CM 41950(1)	_____
<i>Elaphe guttata</i>	CM 41951(7)	_____
<i>Elaphe obsoleta</i> ¹	CM 41952(151)	CM 41952(20)
* <i>Lampropeltis calligaster</i>	CM 41953(1)	_____
* <i>Lampropeltis getulus</i>	CM 41954(46)	CM 41954(5)
<i>Lampropeltis triangulum</i> ¹	CM 41955(2)	_____
* <i>Pituophis melanoleucus</i> ¹	CM 41956(3)	CM 41956(3)
<i>Agkistrodon contortrix</i> ¹	CM 41957(59)	CM 41957(6)
<i>Crotalus horridus</i> ¹	CM 41958(1289)	CM 41958(333)

Discussion.—Charcoal from Unit A, 1.5 m above the boundary with Unit B, was dated at 11,300 ± 1000 yr BP (Y-727) (Guilday et al., 1964:132).

Table 2.—Average stratigraphic depth (m) and current range limits of New Paris No. 4 fossil herptiles.

Mean depth	Taxon	Current range (degrees north latitude)					
		40	45	50	55	60	65
2.6	<i>Coluber constrictor</i>	_____					
2.7	<i>Nerodia sipedon</i>	_____					
3.7	<i>Lampropeltis triangulum</i>	_____					
3.8	<i>Lampropeltis getulus</i>	_____					
3.9	<i>Regina septemvittata</i>	_____					
4.1	<i>Pituophis melanoleucus</i>	_____					
4.5	<i>Agkistrodon contortrix</i>	_____					
4.7	<i>Thamnophis sauritus</i>	_____					
4.8	<i>Crotalus horridus</i>	_____					
5.0	<i>Elaphe guttata</i>	_____					
5.0	<i>Storeria occipitomaculata</i>	_____					
5.1	<i>Elaphe obsoleta</i>	_____					
5.2	<i>Carphophis amoenus</i>	_____					
5.2	<i>Virginia valeriae</i>	_____					
5.2	<i>Diadophis punctatus</i>	_____					
5.5	<i>Rana pipiens</i>	_____					
5.5	<i>Rana sylvatica</i>	_____					
5.6	<i>Ambystoma maculatum</i> -group	_____					
5.6	<i>Rana clamitans</i>	_____					
5.7	<i>Notophthalmus viridescens</i>	_____					
5.8	<i>Eurycea</i> sp.	_____					
5.8	<i>Plethodon</i> -type	_____					
5.9	Desmognathinae	_____					
6.1	<i>Thamnophis sirtalis</i>	_____					
6.3	<i>Storeria dekayi</i>	_____					
6.6	<i>Bufo americanus</i>	_____					
7.0	<i>Hyla crucifer</i>	_____					
7.2	<i>Rana palustris</i>	_____					

The newly identified animals are ecologically compatible with the rest of the herpetofauna, which is now widely distributed in eastern North America. Five snake species now extirpated from the locality are sympatric in the southern Appalachians. *Regina septemvittata*, *Ophedrys aestivus*, *Lampropeltis calligaster*, and *L. getulus* range further north in the Coastal Plain-Piedmont and/or Appalachian Plateau than in the Valley and Ridge Province, indicating topographic control on distributional limits through the Holocene. Other factors have caused the southerly range retraction of *Pituophis melanoleucus*, which exhibits the opposite pattern—northernmost regional distribution in the Valley and Ridge Province 100 km south of New Paris. It remains unclear why the ranges of these five species no longer include the New Paris area.

When arrayed by mean depth in the deposit and maximum current northern range limits, the mammalian component above 5.9 m in the New Paris No. 4 deposit is relatively temperate (50°N latitude or less) in character, below 5.9 m boreal (Guilday et al., 1964:178, table 390. Treating the herptiles in the same manner for comparison (Table 2), the change is similar although less pronounced and higher in the section. Above 5.5 m only two of 15 taxa range north beyond 50°, below 5.5 m 11 of 13 have north limits at or beyond 50°. Ten of 14 mammal taxa found in the lowest meter of the section are present today at Great Whale River, Québec, at the boundary of the Arctic and Hudsonian life zones (Guilday et al., 1964:179). Only two amphibians from the lowest meter, *Rana sylvatica* and *Bufo americanus*, occur with these mammals at Great Whale River. *Rana*

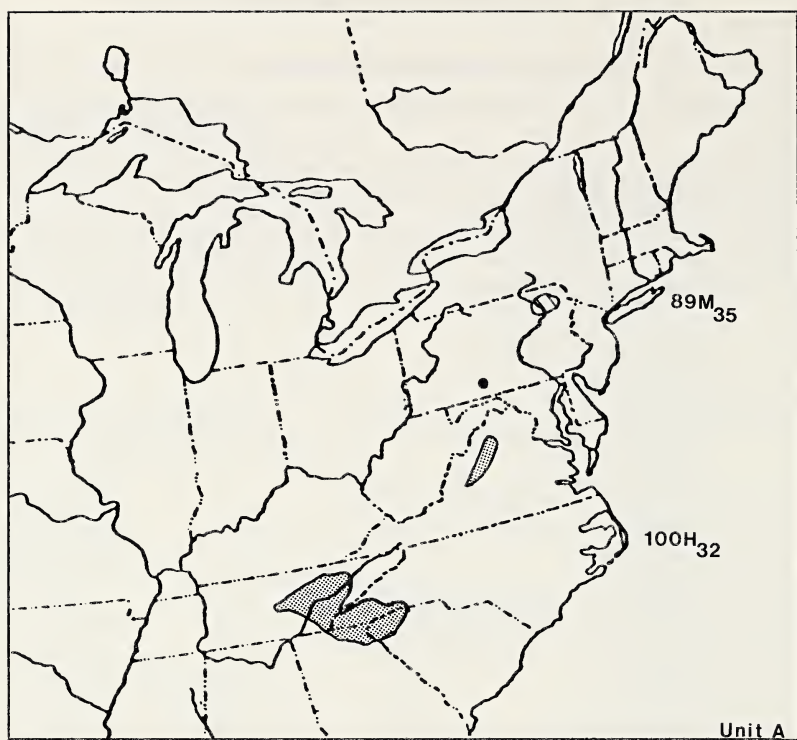


Fig. 3.—Sympatry maps for New Paris No. 4 local faunules. Symbols as in Fig. 2.

pipiens and *Thamnophis sirtalis* range almost as far north, but the other three herptiles of the lowest meter at New Paris do not have northern limits within the boreal zone. All seven have widespread distributions that also include the New Paris locality today, but five of the 14 mammals are not resident in the New Paris area, emphasizing the zoogeographic anomaly between vertebrate classes.

Unit A vertebrates comprise a temperate fauna with a partial mammalian sympatry (31 of 35 extant taxa—89%) in the Pocono Mountains of northeastern Pennsylvania and two sympatric areas for all 32 herptiles in the Virginia Blue Ridge Mountains and at the southern end of the Appalachians in North and South Carolina, Tennessee, and Georgia (Fig. 3A). The partial sympatry for Unit B mammals (Fig. 3B) tells a conflicting story. Consisting of three isolated segments spread through the central and southern Appalachians, only 82% (27 of 33) extant taxa are included. Of Unit B mammals, 15% are boreal, 3% steppe. This is a classic disharmonious faunule, once again contrasting sharply with co-occurring herptiles.

The bird component of New Paris No. 4 is small. Of seven species, only one (*Pedioecetes phasianellis*) has a boreal distribution that does not reach south-central Pennsylvania now.

Guilday et al. (1964:188) assert that the boreal biota of New Paris No. 4 does not support the view (fide Braun, 1950) that the central Appalachians provided a refugium for temperate plants and animals during the late glacial (ca. 15,000–10,000 yr BP). Completed study of the New Paris No. 4 herptiles compromises this statement, as all 32 herptile taxa now live at or further south than New Paris.

All New Paris No. 4 herptiles are small enough to have been prey items for raptorial birds or other predators. Many of the taxa live in or near cave mouths and fissures. It is difficult to determine if herptiles in a fossil accumulation were contributed through predation, accidental falls, or attrition of residents at the accumulation site. Large predatory herptiles, such as the rattlesnakes and garter snakes that dominate the New Paris herpetofauna, very likely denned in the New Paris sinkholes and accumulated there either by attrition over many seasons or during one or more short-term environmental crises. It has not been determined if such hibernaculum mortality types can be distinguished, especially in sinkholes where rate of sedimentation is not readily discerned.

Natural Chimneys

Location.—Augusta County, Virginia, latitude 38°22'N, longitude 78°05'W.

Accumulation.—Raptor roost.

Fauna.—The Natural Chimneys herpetofauna was first reported by Richmond (in Guilday, 1962) with 17 taxa, of which I reject three (*Hyla* sp. CM 7609 [1 ilium] assigned to *Scaphiopus holbrooki*, *Masticophis flagellum* CM 7596 [1 trunk vertebra] to *Coluber* or *Masticophis*, *Crotalus* cf. *adamanteus* CM 7614 [1 trunk vertebra] to *Crotalus horridus*). I have identified 27 additional taxa (including 16 species from Richmond's genera) for a total of 41 herptiles. This expansion results from new material collected in 1977 as well as re-examination of the original collection.

<i>Notophthalmus viridescens</i> ¹	CM 7611(10)
<i>Ambystoma maculatum</i> -group	CM 7612(14)
<i>Ambystoma opacum</i> -group (Tihen, 1958)	CM 41903(2)

* <i>Ambystoma tigrinum</i>	CM 41904(5)
<i>Desmognathinae</i>	CM 7610(2)
<i>Gyrinophilus porphyriticus</i>	CM 41905(11)
<i>Pseudotriton</i> sp.	CM 41906(51)
<i>Eurycea</i> sp.	CM 41907(25)
<i>Plethodon</i> -type	CM 41908(349)
<i>Scaphiopus holbrooki</i> ¹	CM 7606(8), 7609(1)
<i>Bufo americanus</i>	CM 7605(60)
<i>Bufo woodhousei fowleri</i>	CM 41909(9)
<i>Rana catesbeiana</i> ¹	CM 7608(3)
<i>Rana clamitans</i>	CM 41910(6)
<i>Rana ?palustris</i> ¹	CM 7607(5)
* <i>Rana pipiens</i> -group ¹	CM 41911(130)
<i>Rana sylvatica</i>	CM 41912(22)
<i>Chelydra serpentina</i> ¹	CM 7589(1)
<i>Terrapene carolina</i> ¹	CM 41915(4)
<i>Sceloporus undulatus</i> ¹	CM 7603(9)
* <i>Scincella lateralis</i>	CM 41916(1)
* <i>Nerodia ?erythrogaster</i>	CM 41917(1)
<i>Nerodia sipedon</i>	CM 7592(20)
? <i>Regina septemvittata</i>	CM 41918(2)
<i>Storeria dekayi</i>	CM 41919(1)
<i>Storeria occipitomaculata</i>	CM 41920(9)
<i>Thamnophis sirtalis</i> ¹	CM 7591(346)
<i>Thamnophis</i> sp.	CM 41921(151)
* <i>Virginia striatula</i>	CM 41922(1)
<i>Virginia valeriae</i>	CM 41923(10)
<i>Carphophis amoenus</i> ¹	CM 7602(5)
<i>Diadophis punctatus</i> ¹	CM 7600(27)
<i>Coluber</i> or <i>Masticophis</i>	CM 7590(57), 7594(1), 7596(1)
<i>Opheodrys vernalis</i>	CM 41924(3)
<i>Cemophora coccinea</i>	CM 41925(1)
<i>Elaphe guttata</i> ¹	CM 7595(15)
<i>Elaphe obsoleta</i>	CM 41926(4)
<i>Lampropeltis getulus</i>	CM 7597(7)
<i>Lampropeltis triangulum</i> ¹	CM 7593(161)
<i>Agkistrodon contortrix</i> ¹	CM 41927(7)
<i>Crotalus horridus</i> ¹	CM 7601(88), 7614(1)

Discussion.—Guilday (1962) considered the Natural Chimneys sample heterochronic, having accumulated over thousands of years. If this was the case, the composition of the local fauna did not change during the interval of deposition. That is, no disharmonious elements (beyond the boreal + temperate admixture, discovered to be synchronous since Guilday's 1962 paper) are recorded. Of the four extinct mammals from Natural Chimneys, two are large subspecies of living forms (*Tamiasciurus hudsonicus tenuidens* Guilday et al., 1964 and *Eptesicus fuscus grandis* Guilday, 1967) and two became extinct at the end of the Wisconsinan or early in the Holocene (*Castoroides ohioensis* 10,230 ± 150 yr BP, *Mylohyus nasutus* 9410 ± 155 yr BP; Mead and Meltzer, 1984:446, Table 19.4). Thus, Guilday's biochronologic assessment of earliest Holocene age for the Nat-

ural Chimneys local fauna is a minimum date, according to radiometric dating of congeneric material from other localities.

The most important change in the herpetofaunal list is the rejection of *Masticophis flagellum* and *Crotalus adamanteus*. The Natural Chimneys herpetofauna has been considered a southern association, in strong contrast with the boreal and temperate mammal and bird component (Guilday, 1962; Lundelius et al., 1983). In the corrected list, all herptiles reach the latitude of Natural Chimneys, but five taxa (*Rana pipiens*-group, *Ambystoma tigrinum*, *Scincella lateralis*, *Nerodia erythrogaster*, and *Virginia striatula*) no longer inhabit the Valley and Ridge Province in Virginia. Of the five, *Rana pipiens*-group distribution surrounds the area on all sides, while the others occur to the east in the Piedmont (*S. lateralis* and *V. striatula*) and Coastal Plain (*A. tigrinum* and *N. erythrogaster*) or to the west on the Appalachian Plateau (*S. lateralis*) and in the Central Lowlands of the Midwest (*A. tigrinum* and *N. erythrogaster*). All five are widely distributed in the Carolinian Biotic Province, but not closely linked with the Austroriparian Province as are *M. flagellum* and *C. adamanteus*.

The herptile partial sympatry (Fig. 4) is located in the same southern Appalachian area as those of New Paris No. 4. Two of the three members of the fossil sample not present in the sympatry are now excluded from the Valley and Ridge Province, although their nearest range limit is within 50 km of the sympatry. *Opheodrys vernalis* currently occupies the fossil locality but not the sympatry area. A southern shift of a portion of the herptile association after Natural Chimneys time is indicated, although not the more extreme shift previously assumed, i.e., no truly austroriparian element is involved.

The mammal partial sympatry (Fig. 4), like that of New Paris No. 4, is located in northeastern Pennsylvania, but with a greater number of taxa present from Natural Chimneys (47 of 50 extant taxa from NC, 27 of 33 from NP4 Unit B, 31 of 35 from NP4 Unit A). The zoogeography of the Natural Chimneys local fauna indicates it is younger than New Paris No. 4 (Guilday, 1962).

It has been stated that the herptiles of Natural Chimneys disagree with the mammals (Lundelius et al., 1983) in a paleoenvironmental sense. A literal interpretation of decreased annual temperatures (or summer extremes) based on mammals and increased annual temperatures (or length of warm season) based on herptiles is indeed contradictory, but within the paradigm of climatic equability. All vertebrate classes from Natural Chimneys indicate climatic conditions that allowed species now occupying widely disparate habitats to exist in sufficient proximity for their remains to be preserved at a single locality.

Clark's Cave

Location. — Bath County, Virginia, latitude 38°05'10"N, longitude 79°39'25"W.

Accumulation. — Raptor roost.

Fauna. — The Clark's Cave herpetofauna was partially reported in Guilday et al. (1977). Their list includes 14 taxa, ranging in rank from species to family. I have added 33 identifications (all from higher taxa previously listed) for a total of 42 herptile taxa.

<i>Notophthalmus viridescens</i>	CM 41872(24)
<i>Ambystoma maculatum</i> -group	CM 41873(148)
<i>Ambystoma opacum</i> -group	CM 41874(1)
<i>Ambystoma</i> sp. ³	CM 29692(122)



Fig. 4.—Sympatry map for Natural Chimneys local fauna. Symbols as in Fig. 2.

<i>Desmognathinae</i>	CM 41875(94)
<i>Gyrinophilus porphyriticus</i>	CM 41876(2)
<i>Pseudotriton</i> sp.	CM 41877(8)
<i>Eurycea</i> sp.	CM 41878(20)
<i>Plethodon</i> -type	CM 41879(256)
<i>Scaphiopus holbrookii</i>	CM 41880(1)

<i>Bufo americanus</i>	CM 29582(273)
<i>Bufo woodhousei fowleri</i>	CM 41881(7)
<i>Hyla crucifer</i> ³	CM 29581(37)
<i>Rana catesbeiana</i> ³	CM 29574(7)
<i>Rana clamitans</i> ³	CM 29575(3)
<i>Rana palustris</i> ³	CM 29578(40)
<i>Rana pipiens-group</i> ³	CM 29577(35)
<i>Rana sylvatica</i> ³	CM 29579(83)
* <i>Graptemys geographica</i>	CM 29695(1)
<i>Sceloporus undulatus</i> ⁴	CM 29584(13)
<i>Eumeces ?laticeps</i> ⁴	CM 29585(2)
<i>Nerodia sipedon</i>	CM 41882(37)
? <i>Regina septemvittata</i>	CM 41883(1)
<i>Storeria dekayi</i>	CM 41884(86)
<i>Storeria occipitomaculata</i>	CM 41885(61)
<i>Thamnophis ?sauritus</i>	CM 41886(9)
<i>Thamnophis sirtalis</i>	CM 41887(366)
* <i>Virginia striatula</i>	CM 41889(19)
<i>Virginia valeriae</i>	CM 41890(16)
<i>Carphophis amoenus</i>	CM 41891(49)
<i>Diadophis punctatus</i>	CM 41892(124)
<i>Heterodon platyrhinos</i>	CM 41893(3)
<i>Coluber</i> or <i>Masticophis</i>	CM 41894(12)
<i>Opheodrys aestivus</i>	CM 41895(47)
<i>Opheodrys vernalis</i>	CM 41896(6)
* <i>Cemophora coccinea</i>	CM 41897(6)
<i>Elaphe guttata</i>	CM 41898(9)
<i>Elaphe obsoleta</i>	CM 41899(10)
<i>Lampropeltis calligaster</i>	CM 41900(4)
<i>Lampropeltis getulus</i>	CM 41901(9)
<i>Lampropeltis triangulum</i>	CM 41902(78)
<i>Crotalus horridus</i>	CM 29694(5)

Discussion.—The mammals of Clark's Cave are very similar to those of New Paris No. 4, indicating an age assessment for the Clark's Cave local fauna of ca. 11,000 yr BP (Guilday et al., 1977). The herpetofauna is more similar to that of Natural Chimneys than New Paris No. 4, but the difference may not be significant, because diversity is less in the New Paris sample than in the other two.

Four reptiles (*Graptemys geographica*, *Virginia striatula*, *Cemophora coccinea*, and *Lampropeltis calligaster*) plus the *Rana pipiens-group* frogs do not presently occur at the locality. The average distance by which they are removed from Clark's Cave is 90 km and the most distant herptile, the leopard frog, is no more than 125 km away. This minor disjunction requires little invocation of climatic change. Periodic fluctuations of range limits in response to various short-term edaphic or biotic perturbations (as yet undiscovered from the fossil or climatic proxy records) or even insufficient documentation of true ranges may explain the extirpation. The Clark's Cave fossil herptiles have a partial sympatry in the Great Smoky Mountains (Fig. 5). Two snakes do not reach this sympatry; *Opheodrys vernalis* 250 km to the north and *Virginia striatula* 100 km to the south, in the same pattern of disjunction as for Natural Chimneys. This appears to be a small-scale version of climatic equability, with taxa from both north and south indicating



Fig. 5.—Sympatry map for Clark's Cave local fauna. Symbols as in Fig. 2.

reduced climatic extremes. However, with only three snake species involved between two localities, I consider this not a case of climatic equability, as the taxa in question do co-exist elsewhere within their ranges. It is an example of individualistic response to local microhabitat availability. The partial sympatry area for Natural Chimneys and Clark's Cave plus one of the complete sympatry areas for New Paris No. 4 includes the Great Smoky Mountains. This likely reflects

surviving habitat diversity in that area rather than a single set of ecologic conditions suitable for all taxa, as a consequence of unit-fauna retreat from western Virginia and Pennsylvania.

Fifty-two percent of the Clark's Cave fossil mammal taxa do not presently occur in the central Appalachians, live only at higher elevations in the region, or are of sizes indicating boreal rather than temperate populations (Guilday et al., 1977). Seven percent of the avifauna does not presently spend any part of the year in the central Appalachians (Guilday et al., 1977). Why can every herptile of the local fauna still be found within 125 km after 11,000 years of climatic and biotic change that has driven out several birds and many mammals? Climatic equability is not the best answer, as northern herptiles were apparently not present and only a slight southward shift of those represented as fossils is evident.

Baker Bluff Cave

Location.—Sullivan County, Tennessee, latitude 36°27'30"N, longitude 82°28'00"W.

Accumulation.—Raptor roost.

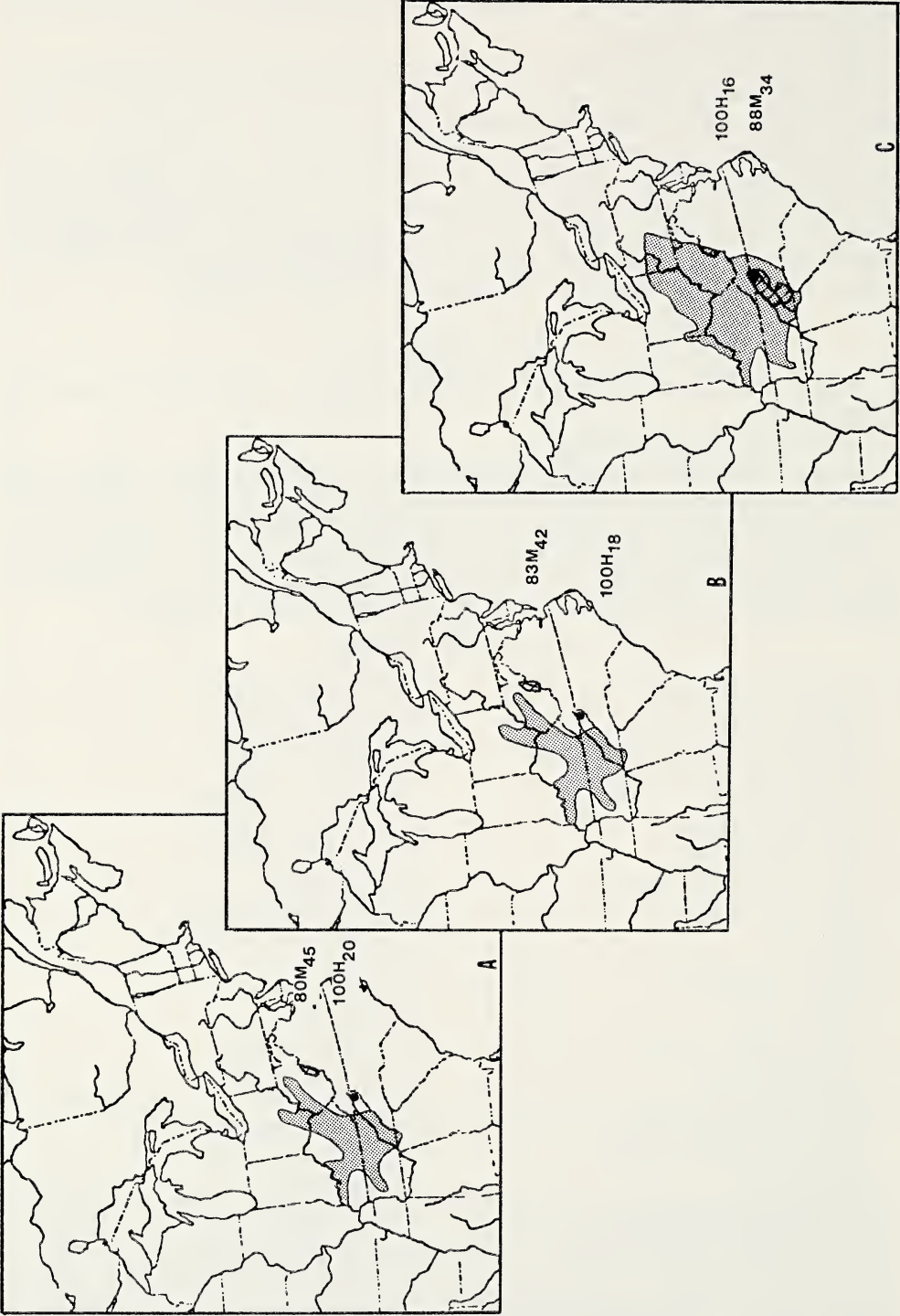
Fauna.—Only minor changes to Van Dam's (1978) faunal list are made in this review. 22 taxa are recorded from the mid-levels of Baker Bluff Cave, the interval comparable to the time of deposition for the other herpetofaunas of this study.

Taxonomic changes from Van Dam (1978) for all levels are as follows: *Ambystoma opacum* altered to *A. opacum*-group, *Desmognathus* sp. to *Desmognathinae*, *Hyla* sp. CM 29802 (1 left ilium) assigned to *Bufo* sp. juvenile.

mid-levels (5–7 ft) only

<i>Cryptobranchus alleganiensis</i> ⁵	CM 29776–777(42)
<i>Necturus maculosus</i> ⁵	CM 29770–771(8)
<i>Ambystoma maculatum</i> -group ⁵	CM 29759–760(7)
<i>Ambystoma opacum</i> -group ⁵	CM 29755–756(6)
<i>Ambystoma</i> sp. ⁵	CM 29763–764(14)
<i>Desmognathinae</i> ⁵	CM 29782–783(176)
<i>Bufo americanus</i> ⁵	CM 29788–789(30)
<i>Bufo woodhousei fowleri</i> ⁵	CM 29795(6)
<i>Rana sylvatica</i> ⁵	CM 29805–806(14)
<i>Rana</i> sp. ⁵	CM 29811–812(3)
<i>Eumeces fasciatus</i> ⁵	CM 29817(1)
<i>Nerodia sipedon</i> ⁵	CM 29852(3)
<i>Nerodia</i> sp. ⁵	CM 29853(1)
<i>Thamnophis sirtalis</i> ⁵	CM 29859–860(3)
<i>Thamnophis</i> sp. ⁵	CM 29863–864(5)
<i>Diadophis punctatus</i> ⁵	CM 29830(6)
<i>Heterodon platyrhinos</i> ⁵	CM 29825–826(2)
<i>Coluber</i> or <i>Masticophis</i> ⁵	CM 29834–835(10)
? <i>Elaphe</i> sp. ⁵	CM 29849(3)
* <i>Lampropeltis getulus</i> ⁵	CM 29846(6)
<i>Lampropeltis triangulum</i> ⁵	CM 29840–841(16)
<i>Crotalus horridus</i> ⁵	CM 29820–821(36)

Discussion.—This stratified local fauna ranges in age from 19,100 ± 100 yr BP to 200 yr BP (Guilday et al., 1978:53). The mid-levels date from approximately



10,560 to 11,640 yr BP (Guilday et al., 1978:53). Seventy-two percent of the Baker Bluff herptile taxa (18 of 25) are recorded in the mid-levels.

All but one of the herptiles presently live in the immediate area. *Lampropeltis getulus* has its nearest range limit only 65 km east of the locality. All the taxa are widely sympatric through the Appalachian Plateau west of Baker Bluff (Fig. 6B). A slight increase in effective precipitation compared to the present condition is indicated by this zoogeographic shift.

Van Dam (1978) asserted that no discernible trends occur in the herpetofauna that reflect ecologic or climatic change through the past 20,000 years in north-eastern Tennessee. Sympatry maps for the three faunules (Fig. 6A–C) support Van Dam's conclusions. The mammal partial sympatry is located in the same area as the middle of the three areas for New Paris No. 4 Unit B (Fig. 3B). Although the sympatry area remains in the same location, the percentage of Baker Bluff mammal taxa participating decreases from ca. 20,000 to 200 yr BP.

Kingston Saltpeter Cave

Location. —Bartow County, Georgia, latitude 34°12'18"N, longitude 84°54'55"W.

Accumulation. —Cave/?raptor roost.

Fauna. —Preliminary reports on Kingston Saltpeter Cave (Blair et al., 1981; Sneed, 1981) include partial lists of vertebrates recovered. The 43 herptile taxa reported here comprise the first comprehensive listing from the local fauna. *Storeria* sp. refers to damaged vertebrae that may represent *S. dekayi*, *S. occipitomaculata*, or even *Virginia* spp. A complete study of the paleontology and history of the cave is underway.

<i>Notophthalmus viridescens</i>	BC 35(2)
<i>Ambystoma maculatum</i> -group	BC 36(46)
<i>Ambystoma opacum</i> -group	BC 37(80)
<i>Ambystoma tigrinum</i>	BC 38(26)
Desmognathinae	BC 40(33)
<i>Pseudotriton ruber</i>	BC 43(7)
<i>Eurycea</i> sp.	BC 42(10)
<i>Plethodon</i> -type	BC 41(302)
<i>Scaphiopus holbrooki</i>	BC 44(19)
<i>Bufo americanus</i>	BC 45(33)
<i>Bufo woodhousi fowleri</i>	BC 46(4)
<i>Hyla crucifer</i>	BC 48(1)
<i>Gastrophryne carolinensis</i>	BC 49(15)
<i>Rana catesbeiana</i>	BC 50(21)
<i>Rana clamitans</i>	BC 51(2)
<i>Rana pipiens</i> -group	BC 52(72)
<i>Rana</i> sp.	BC 53(47)
Kinosternidae	BC 54(2)
<i>Chrysemys picta</i>	BC 55(8)
*? <i>Clemmys insculpta</i> or ? <i>Pseud- emys concinna</i>	BC 57(1)

←

Fig. 6.—Sympatry maps for Baker Bluff Cave local faunules. A—upper levels (200 yr BP–10,560 rcybp), B—mid levels (10,560–11,560 rcybp), C—lower levels (11,640–19,100 rcybp). Symbols as in Fig. 2.

<i>Pseudemys ?concinna</i> or <i>Pseud-</i>	BC 58(1)
<i>emys ?scripta</i>	
<i>Terrapene carolina</i>	BC 56(40)
<i>Anolis carolinensis</i>	BC 59(11)
<i>Sceloporus undulatus</i>	BC 60(6)
<i>Scincella lateralis</i>	BC 61(1)
<i>Nerodia sipedon</i>	BC 62(70)
<i>Storeria dekayi</i>	BC 63(6)
? <i>Storeria</i> sp.	BC 64(31)
<i>Thamnophis ?sauritus</i>	BC 65(41)
<i>Thamnophis sirtalis</i>	BC 66(156)
<i>Virginia striatula</i>	BC 68(5)
<i>Virginia valeriae</i>	BC 69(2)
<i>Carphophis amoenus</i>	BC 70(1)
<i>Diadophis punctatus</i>	BC 71(7)
<i>Coluber</i> or <i>Masticophis</i>	BC 72(21)
<i>Opheodrys ?aestivus</i>	BC 73(3)
<i>Elaphe guttata</i>	BC 74(23)
<i>Elaphe obsoleta</i>	BC 75(32)
<i>Lampropeltis calligaster</i>	BC 76(16)
<i>Lampropeltis getulus</i>	BC 77(10)
<i>Lampropeltis triangulum</i>	BC 78(15)
<i>Pituophis melanoleucus</i>	BC 79(15)
<i>Agkistrodon contortrix</i>	BC 80(10)

Discussion.—Bone collagen from this local fauna was dated at $10,300 \pm 130$ yr BP (Beta 12771). The herpetofauna is sympatric and currently occupies much of northern Alabama and the northwestern corner of Georgia near the fossil locality (Fig. 7). Climatic requirements for southern Appalachian herptiles were nearly equivalent to modern conditions at the close of the Wisconsinan Age.

The fossil accumulation was recovered from cave earth matrix dissimilar to the surficial regolith (fissure fills) in which nearby Ladds Quarry local fauna was found (J. A. Holman, personal communication, July 1985). The two herpetofaunas are similar except for five extralimital records and *Geochelone crassiscutata*, an extinct giant land tortoise, at Ladds (Holman, 1985a). As the local faunas are nearly contemporaneous (Ladds dates: $10,940 \pm 210$ and $10,290 \pm 100$ yr BP; Holman, 1985b), taphonomic factors as yet undiscovered must be responsible for the faunal differences.

The Kingston fossil mammals are characteristic of high elevation habitats of the central Appalachians (Fig. 7), with only one boreal (*Phenacomys intermedius*) and one southern (*Panthera onca*) species (Fay and Wilson, in preparation). A similar, disharmonious association has been reported from Ladds Quarry (Ray, 1967; Lundelius et al., 1983).

DISCUSSION

Why are temperate herptiles found in association with boreal + temperate birds and mammals in Appalachian local faunas? The lack of boreal herptiles in the Late Wisconsinan fossil record may be due to the nature of potential migrants forced out of northeastern North America by glacial ice. There are only two "boreal" herptiles (defined here as occurring mostly within the area of northern hardwood and coniferous forests) that range east of the Great Lakes and north of

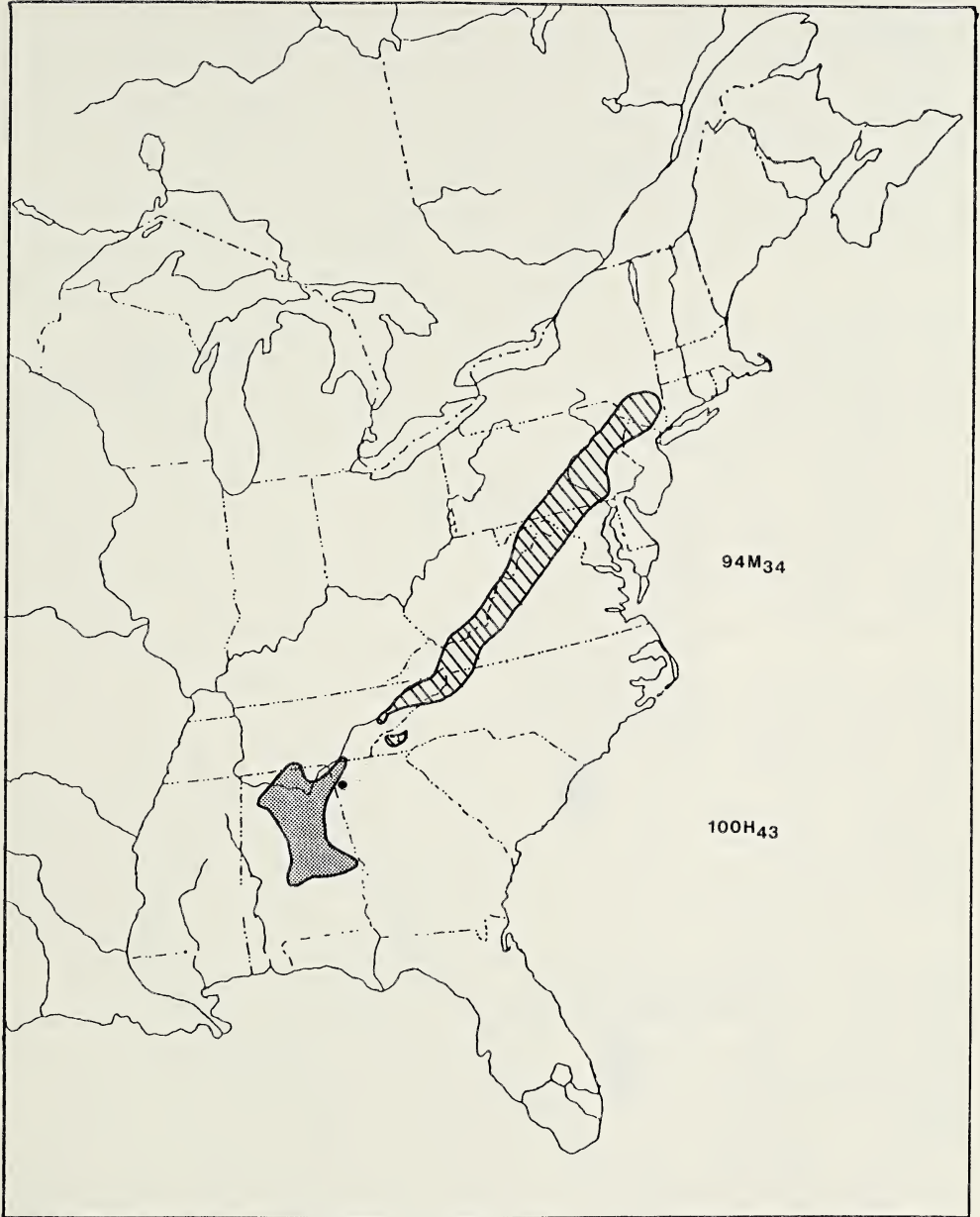


Fig. 7.—Sympatry map for Kingston Salt peter Cave local fauna. Symbols as in Fig. 2.

central Pennsylvania (i.e. north of the southern and central Appalachian region of this study) (Fig. 8). *Ambystoma laterale* and *Rana septentrionalis* are difficult to distinguish osteologically from more widely distributed congeners and only *A. laterale* has been reported as fossils (Fay, 1984a). The two species may not appear in the central Appalachian fossil record because (1) They did not evolve before the Holocene, (2) Wisconsinan ice displaced them to another region (e.g., Appalachian Plateau or exposed continental shelf) with a more poorly known fossil

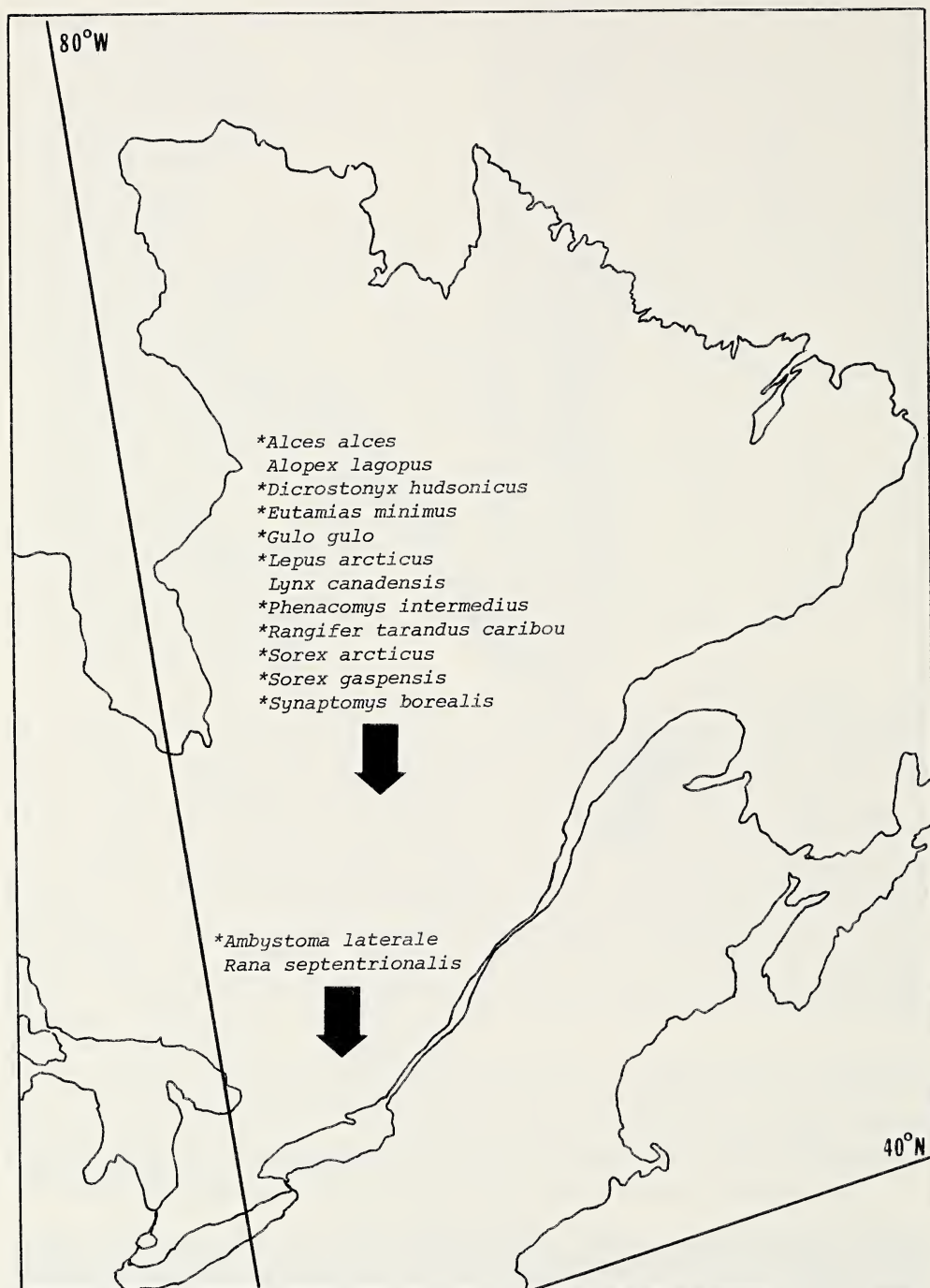


Fig. 8.—Mammals and amphibians with eastern North American range limits presently north of 42°N. Asterisks denote species with Late Wisconsinan–early Holocene fossil record in the Appalachian region.

record, or (3) they were present in the central Appalachians at very low densities or are not distinguishable from congeneric fossils (Fay, 1986). Until identification criteria are devised, these scenarios cannot be tested. Twelve mammals from the same northeastern region, all with fossil records (ten from within that region), do not now range further south in the Appalachians than central Pennsylvania (Fig. 8) (Fay, 1984b, 1986). Many herptile taxa that are partially sympatric in the north with these "boreal" mammals are also widely distributed in more temperate regions, obscuring any boreal vs. temperate indications that might contribute to paleoenvironmental reconstructions. Additional studies of clinal variation within herptile taxa will address this problem.

Extirpated species from these fossil localities may have been excluded by climatic or biotic changes since latest Wisconsinan time. The environment of the central Appalachians has seemingly become unsuitable for these animals, or the method by which they were added to the fossil accumulations no longer operates. Older herpetofaunas of the region also contain extirpated taxa. Three Irvingtonian local faunas (Cumberland Cave, Maryland [Holman, 1977a]; Trout Cave-Lower Level, West Virginia [Holman, 1982]; and Hanover Quarry Fissure, Adams County, Pennsylvania [Fay, in preparation]) include herptiles that have retracted their range limits to the north, west, or east outside the central Appalachians. This suggests a gradual shrinking of species distribution through the Neogene, as one species (*Elaphe vulpina*) is also known from the late-glacial Wisconsinan of Georgia (Holman, 1985a), Pliocene of Idaho (Holman, 1968), and several other now extralimital fossil localities (see Holman, 1979, 1981).

Some eastern North American endemic herptiles, such as *Clemmys muhlenbergi*, *Eumeces a. anthracinus*, *Pseudotriton montanus*, and *Scaphiopus holbrooki*, have discontinuous Appalachian ranges. Two possibilities would explain both their discontinuous ranges and the apparent extirpation of some of these and other taxa since the Late Wisconsinan. Physical and biological factors of central Appalachian habitats may have changed beyond the tolerances of these animals, or current distributions may be incompletely known and the animals actually occupy the entire region in suitable microhabitats. The latter is quite likely for *Clemmys muhlenbergi* (Bury, 1979) and perhaps for *Rana pipiens* (McCoy, 1982).

Zoogeography of the local faunas can be employed to illustrate tentative paleoenvironmental reconstructions (as mentioned previously, details of individual species range changes and modern autecology will strengthen future attempts to define the partial analog). As expected, areas of greatest partial sympatry for mammals and herptiles of all six local faunas (Fig. 2–7) are within the Appalachian Mountains and/or Plateau physiographic provinces. Herptiles "missing" from the sympatries are found within several hundred kilometers in similar or identical habitats. Most extralimital mammals, on the other hand, now range no closer to the sympatries than eastern Canada and many are removed over 1000 km to the west or northwest. Birds of these local faunas are not included on the maps because of low species diversity for most samples. They do, however, follow the mammalian pattern of regional + extralimital ("boreal") habitat distribution.

Mammal partial sympatries are situated further north than both herptile sympatry and fossil locality for all but the three oldest faunules illustrated (Frankstown Cave, Fig. 2; New Paris No. 4, Unit B, Fig. 3B; Baker Bluff Cave lower levels, Fig. 6C). Frankstown and Baker Bluff lower levels are the only faunules with overlapping herptile-mammal sympatries, and the latter is the only instance in which maximum partial sympatry includes the fossil locality. This pattern implies

that environmental conditions prior to ca. 12,000 yr BP were more similar to the present than latest Wisconsinan environments.

Herptile sympatries for the Pennsylvania and Virginia faunules (excluding the pre-latest Wisconsinan Frankstown Cave and New Paris No. 4, Unit B) are located 150 to 750 km south of the fossil localities (Fig. 3A, 4, 5), while sympatries for the Tennessee and Georgia faunules are at the same latitude and within 50 km of the localities (Fig. 6B, 7). For the Pennsylvania and Virginia faunules, herptiles appear to represent the environments of the Great Smoky Mountains near the south end of the Appalachian region, while mammals (extra-regionals excluded) are characteristic of Pocono Mountain environments at the north end of the central Appalachians. For Baker Bluff mid levels (Fig. 6B), mammals are characteristic of central Appalachian environments while herptiles appear to be shifted west onto the Appalachian Plateau (due to small sample size). Kingston exhibits a mammal pattern unique among these faunas, spanning the entire central Appalachians (Fig. 7). It is also the only local fauna of this study with species now occurring far to the north (*Phenacomys intermedius*) and south (*Panthera onca*) (Fay and Wilson, in preparation).

A "step" in the Late Wisconsinan climatic gradient apparently existed between northern Tennessee and west-central Virginia, producing these zoogeographic patterns. At 10,000 yr BP, the boundary between mixed conifer-northern hardwoods and deciduous forest vegetation types occurred in this area (Delcourt and Delcourt, 1981). North of this "step," some herptiles have been forced southward or out of the Valley and Ridge Province by climatic change since the latest Wisconsinan, while little range adjustment occurred south of the "step."

CONCLUSIONS

Late Wisconsinan herpetofaunas show different, less dramatic Wisconsinan-Holocene range adjustments than the birds and mammals from the same local faunas. No herptiles from these six localities have left the region or are now extinct. Twenty-eight birds and mammals from the combined faunal list are now extirpated from the fossil localities, 17 mammals and one bird are extinct. In 1965 it was possible to state: "The fluctuating ecological conditions during the Pleistocene must have modified the distribution of reptiles more than that of mammals or birds living in the same geographic area" (Auffenberg and Milstead, 1965:557). With the increasing number of herpetofaunas available for study, this view is no longer tenable for eastern North America. Even with the evidence at hand and previous statements (Smith, 1957:207) to the contrary, herptiles that do not match the bird and mammal reconstructions are dismissed in the current literature; "... the (Clark's Cave) herpetofauna is similar to that of the area today, with several species ... that would have been *unable to survive* the 'boreal' conditions postulated for the area on the basis of the mammalian fossil fauna" (Lundelius et al., 1983:316 and 324; emphasis added). There is no evidence for the implication that the herptiles are heterochronic intrusions into the fossil accumulations (Fay, 1984b; Holman, 1986) or that temperate herptiles *must be* ecologically incompatible with "boreal" birds and mammals. In fact, the "boreal" nature of these local faunas may have been over-emphasized. Although many taxa represented by fossils now range further north than the Appalachian localities, no more than 18% of the mammal taxa (at New Paris No. 4, Unit B) are restricted to latitudes north of the central Appalachians.

A number of alternative explanations, several already alluded to in this study,

may be advanced based on zoogeography, taxonomy, and ecology of Appalachian herptiles (Fay, 1986). (1) There are fewer eastern North American boreal herptiles than mammals that could be displaced by glaciation to form a boreal + temperate association. (2) It is apparent from the discussion of plethodontid salamanders that several herptile genera and many species, including relatively "boreal" ones, go unrecognized in the fossil record because of osteological similarity to more widespread taxa. (3) Herptiles did not respond as strongly to glacial-interglacial climatic changes as did other vertebrates. Herptiles have a marked capacity for acclimatization to seasonal climatic change that may also provide the ability to adapt to progressive, long term change by alterations in physiology or behavior rather than distribution. (4) Much of the herpetofauna of the central and southern Appalachians has its center of distribution here, reflecting probable center of origin and/or restricted microhabitat requirements for many of the species. In other words, the animals have endured in suitable local environments since first evolving, in spite of general changes in climate and biota. The southern and central Appalachian region, once thought to be the refugium for the entire eastern temperate biota (Braun, 1950), held individual taxa or enclaves of plants (Davis, 1983a, 1983b). The region also "shielded" the herpetofauna in whole or in part from glacial climates. The preceding statements are not strongly documented as yet, but are intended as directions for further investigations into the neontology as well as paleontology of the Appalachian herpetofauna.

An hypothesis that explains the admixture of faunal elements in Quaternary fossil accumulations that are not now sympatric is that of increased climatic equability compared to the strongly continental climate prevailing over much of North America now. Milder winters are implied, allowing southerly distributed taxa to expand northward, as well as cooler summers permitting northerly distributed taxa to disperse southward (Holman, 1976 and references therein). Although giant tortoises were a stimulus to the development of the hypothesis (Hibbard, 1960), only a few attempts have been made to evaluate climatic equability in regard to the Quaternary herpetofaunal record (Holman 1976, 1977b, 1980).

Rhodes (1984) asserts that it is unnecessary to invoke climatic equability for local faunas containing a greater number of boreal, fewer temperate-mesic, and no more-southern forms than occupy the locality today. Increased microclimatic contrast between slope exposures may have been sufficient to allow range overlaps of boreal and temperate animals. No "southern" mammal component that would indicate milder winters (with possible exception of *Dasypus*, *Mylohyus*, *Platygonus*, and *Tapirus*, but see Rhodes [1984] for a dissenting view) occurs in these Late Wisconsinan Appalachian local faunas. Although herpetofaunal sympatry areas are south of three of the six localities of this study, the herpetofaunas contain no true southern (i.e., austroriparian) taxa and the one report of a true boreal taxon *Bufo americanus copei*, is not supported. The only Late Wisconsinan association that includes north and south extralimitals is from Ladds Quarry, Georgia, where *Geochelone* cf. *G. crassus*, *Pseudemys floridana*, and *Bufo terrestris* occur with *Clemmys insculpta* and *Elaphe vulpina* (Holman, 1985a). If climatic equability can be registered in the herptile record for eastern North America, it decayed to the present continental pattern, with this one known exception, by the end of the Wisconsinan Age. It is not yet clear what special circumstances were responsible for the Ladds faunal composition and if other localities may yield similar associations.

At the end of Wisconsinan time, the vegetation from 34°N to 37°N underwent a major change in species composition as boreal plant taxa removed to the north during glacial retreat (12,500 to 9,000 yr BP; Delcourt and Delcourt, 1983). In the latest Wisconsinan–earliest Holocene interval, deciduous forest in the region of the six herpetofaunas reached its highest species richness during relatively cool, equable conditions (Delcourt, 1979).

While mammalian and avian faunal composition altered to adjust from a full-glacial “boreal” environment with tundra, taiga, and boreal forest species present in the region to a post-glacial environment with deciduous forest, the herpetofauna remained almost undisturbed (with a comparatively minor southward shift of sympatry areas for central Appalachian associations) through over 7,000 years of climatic, vegetational, and faunal change. The climatic and biotic changes were within the tolerance limits of most reptiles and amphibians, and/or when used as proxy data, most herptiles represent local microclimate rather than regional macroclimate (re: Bryson, 1985). Future study must determine what partial analogs may be applied in comparing Quaternary herptiles with the remainder of the fossil record.

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FIVE NEW SPECIES AND ONE NEW SUBSPECIES
OF BUTTERFLIES FROM THE SIERRA DE BAORUCO
OF HISPANIOLAKURT JOHNSON¹DAVID MATUSIK²

ABSTRACT

Based on collections from 1981-87 in the Las Abejas region of broadleaf forests on the south slope of the Sierra de Baoruco, Pedernales Province, Dominican Republic, five new species and one new subspecies of butterflies are described. These include *Electrostrymon minikyanos*, *Strymon andrewi*, *Heterosmaitia abeja*, and *Leptotes idealus* (Lycaenidae), new species, and *Panoquina ocola distipuncta* (Hesperiidae), new subspecies. *P. hecebolus* Scudder is also documented from the Antilles for the first time. A new genus, *Terra* (Lycaenidae), is erected for a new species *T. hispaniola* and distinguished from its sympatric sister genus *Nesiostrymon* Clench by a numerical cladistic analysis (PAUP). Range disjunctions between Jamaica and southern Hispaniola in *Heterosmaitia* and *Leptotes* are noted in relation to Caribbean tectonic history and vicariance biogeography.

INTRODUCTION

In 1987, The Carnegie Museum of Natural History (CMNH) sponsored an expedition to the remote broadleaf forests on the south slope of the Sierra de Baoruco, in a region called Las Abejas, Pedernales Province, Dominican Republic, for purposes of collecting all groups of diurnal and nocturnal insects. The expedition followed on collections of Lepidoptera at Las Abejas by Matusik (1981-84) and Matusik and Johnson (1985, 1986), when several new species of butterflies were discovered and a number of unusual moths taken at bait. The purpose of this paper is to characterize previously undescribed butterflies from the region and make names available for forthcoming publications on the Antillean fauna.

Recent publications by Albert Schwartz and his colleagues (Schwartz, 1983a, 1983b, in press; Schwartz and Gali, 1984; Schwartz and Miller, 1985; Gali, 1983, 1985; Gonzalez, 1987; Schwartz and Correa, 1986; Schwartz and Sommer, 1986), and the present authors (Johnson and Matusik, 1986; Johnson et al., 1987) have called attention to the diversity of butterfly taxa occurring on Hispaniola and described various new taxa recently discovered on the island. The Sierra de Baoruco region of the southwestern Dominican Republic comprises part of the original "southern paleoisland" of Hispaniola (Gali and Schwartz, 1983; Schwartz and Gali, 1984; Schwartz and Correa, 1986) and thus has a distinctive fauna. Here, in isolated, mesic forests, occur a virtual "who's who" of "rare" and "exceedingly rare" (Riley, 1975) butterflies. Prior to recent work, many of these taxa had seldom been collected (*Battus zetides* Munroe, *Doxocopa thoe* (Godart), *Anetia jaegeri* (Menetries), *Myscelia aracynthia* (Dalman), *Paratrytone batesi* Bell, *Adelpha gal-*

¹ Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.

² Department of Entomology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.

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ania (Godart), *Greta diaphana galii* Schwartz, *Calisto raburni* Gali). Recent collections in the region have added some half dozen new species to the Hispaniolan fauna (Schwartz et al., 1983–86, see the ten papers cited above).

Our collections at Las Abejas from 1981–87 have included five new species and one distinctive new subspecies of butterflies. The new taxa are described below as a group, arranged taxonomically by family, with each section reviewed by appropriate specialists (see Acknowledgments and Remarks). Brief introductory sections are provided for each family, noting recent research concerning that group on Hispaniola. Each new species is compared in detail with its congeners and male and female genitalic drawings of all taxa are presented. Since the taxa are described in the context of related congeners, an extensive differential diagnosis is provided before each description, citing the relevant literature. In descriptions we follow Ehrlich and Ehrlich (1961) for wing venation and surface features, incorporating for phylogenetic consistency the CuA (cubitus anterior) notation. For certain genitalic structures peculiar to the Lycaenidae we follow Johnson (1976, 1978, 1988). For specimen depositions the following abbreviations are used: Albert Schwartz Collection (ASC), Allyn Museum of Entomology (AME), American Museum of Natural History (AMNH), Carnegie Museum of Natural History (CMNH), David Matusik Collection (DMC), National Museum of Natural History (NMNH). For certain type specimen designations required by the Code of the International Commission on Zoological Nomenclature we quote verbatim from the citations in Bridges (1988).

Las Abejas

“Las Abejas” (Gali and Schwartz, 1983, Schwartz, in press) is a local name applied as a “transect” designation by Ideal Dominicana S.A. (and formerly by Alcoa Exploration Company) to a sector of land located north of an east/west ridge running directly north and west of Aceitillar (found on most maps), proceeding west toward the Haitian border, and north to the border between the provinces of Pedernales and Independencia, Dominican Republic. In fact, conversations with native people living near the region, indicate that the name is applied in the singular (La Abeja). On some local maps the area is indicated as Fondo de Abeja. In this paper, we use the plural, Las Abejas, to be consistent with prior publications on the region. The mesic broadleaf forests in this transect, which occur as enclaves within and along upland escarpments bordering xeric pine forests, are protected as a National Park under the direct supervision of Ideal Dominicana. The forest at Las Abejas may be reached only by walking some 3–5 km, after proceeding as far as possible by vehicle. The most densely forested portion of Las Abejas, called Fondo de Abeja, lies at the compass coordinates of 18°09'N, 71°38'W and extends from an altitude of approximately 1160 m to 1250 m at the margin with upland pine forest. We note three principal collecting localities at Las Abejas which are characterized by distinctive taxa of both butterflies and moths. We summarize these here to allow brief subsequent reference: (1) “lower Abejas”—elevation 1160 m, at the base of the steep slopes, is the wettest area of the basin and covered with dense forest; collecting is difficult except for small clearings; (2) “middle Abejas”—elevation 1190 m, along an ascending path from lower Abejas, is more interspersed with understory. Areas without canopy are frequent in the region 50–100 m below adjacent, pine-covered ridges; (3) “upper Abejas”—elevation 1250 m, is at the abrupt margin between broadleaf forest and pine woodland where the access trail first begins to descend. This area

is sunny and peppered with flowering blackberry bushes (*Rubus*), a rich nectar source for many butterflies.

TAXONOMIC DESCRIPTIONS

Lycaenidae

New lycaenid butterflies from the Antilles are not entirely unusual. In the Theclinae, Comstock and Huntington (1944) distinguished several Hispaniolan taxa and, more recently, Schwartz and Miller (1985) described the very distinctive *Strymon monopeitinus*. We recently described a new *Tmolus* species from Hispaniola, presently known from only two specimens (Johnson and Matusik, in press). Other taxa, like *Tmolus azia* (Hewitson) have only recently been found on the island (Beck, 1983; Schwartz, in press). In the Polyommatainae, Kaye (1931) differentiated the Jamaican endemic *Leptotes perkinsae* from the more familiar *L. cassius* (Cramer) and *L. marina* (Reakirt).

Hairstreak butterflies occur in low density, are often habitat-specific, and because of their small size, are often overlooked by collectors. Of the five species described below, two have been taken by us on Hispaniola since 1984. Two others were first captured in 1986 and a fifth in 1987.

Theclinae

Genus *Electrostrymon* Clench

Clench (1961) erected this genus with the rather unfortunate type species *Papilio endymion* Fabricius (see Hemming, 1967 [*Evenus*, *Hexuropteris*, *Lycaena*]; Miller, 1978; and Miller and Brown, 1981, concerning confusion regarding this name). Since this species is without an unambiguous type specimen and part of a farflung and highly variable assemblage, it is uninformative as a type species. Riley (1975) used the genus to include a large number of Antillean taxa. Undoubtedly such usage is not monophyletic. In 1986 we collected a small undescribed hairstreak at Las Abejas. As might be expected, its morphology was divergent. Thus, the following description of this species in *Electrostrymon* follows Riley's general concept for the genus and must be considered tentative until *Electrostrymon* is more thoroughly studied.

Electrostrymon minikyanos, new species

Fig. 1A, B; 2A

Diagnosis.—This small hairstreak (forewing expanse 10.0 mm) (Fig. 1A, B) differs markedly from any other *Electrostrymon* species known from the Antilles. Though similar to other *Electrostrymon* taxa in its small size, dark lower surface coloration, and lack of male androconial brand, the species is unique in being markedly dull purplish blue on the hindwing uppersurface and forewing base. The undersurface is most like *E. pan* (Drury) (endemic to Jamaica) (Fig. 1F) with a dark basal disc and medial tripartite band. However, the *Thecla*-spot (sensu Clench, 1961, marginal in cell CuA1) in *E. minikyanos* is not of the huge size that characterizes *E. pan* (Fig. 1F). The limbal area of *E. minikyanos* is heavily grizzled with black, interspersed with distinct white spots and patches based on the anal lobe and across the limbal area. Other Antillean endemics *E. angelia* (Hewitson) (Fig. 1E), *E. dominicana* (Lathy) (Fig. 1C), and *E. angerona* (Godman and Salvin) (Fig. 1D), contrast with *E. minikyanos* in having lavish coloration on the under surface limbal areas. Genitalia of *E. minikyanos* (Fig. 2A) differ markedly from



Fig. 1.—LYCAENIDAE. Adults of *Electrostrymon*. A. Upper surface, holotype male, *E. minikyanos*. B. Lower surface, same. C. Lower surface, *E. dominicana*, topotypical male, Canefields, Dominica, 12–16 November 1933, leg. L. E. Chadwick (AMNH). D. Lower surface, *E. angerona*, topotypical male, St. Vincent (AMNH). E. *E. angelia boyeri*, paratype male, Aux Cayes, Haiti, 15–20 March 1922 (AMNH). F. *E. pan*, male, Bellevue, St. Anns, Jamaica, 26 February 1955, leg. B. Heineman (AMNH).

other taxa of *Electrostrymon* (*E. pan*, Fig. 2C, *E. angelia boyeri* (Comstock and Huntington), Fig. 2B) as noted below.

Description.—*Male*. Upper surface of the wings: forewing blackish brown, dull purplish basad. Hindwing dull purplish, submargins distally blackish brown. No androconial brand. Short tail, terminus of vein CuA2. Lower surface of the wings: ground blackish brown. Forewing with median to postmedian blackish line, costa to vein CuA2. Hindwing ground as above, bipartite median line, black basad, white distad. Limbal area with orange *Thecla*-spot, cell CuA1, otherwise grizzled darkly and area strewn with white to whitish patches cells 2A–M3. Length of forewing: 10.0 mm (holotype). *Female*. Unknown. *Male genitalia*. Fig. 2A. Saccus large and triangular, vinculum quite elongate for genus with uncus produced ventro-centrad. Valvae in ventral view with termini rather hook-shaped caudad round and bulbous bilobes (sensu Johnson, 1976, 1978). Aedeagus long, nearly twice length from tip of saccus to labides with single pointed terminal cornutus. A small brush organ extends from the middle of the vinculum to base of labides. *Female genitalia*. Unknown.

Type.—Holotype, male, middle Abejas, 1500 m 1030 hrs, nectaring in sunlight, July 11, 1986, leg. K. Johnson deposited AMNH (AMNH/HS #82).

Remarks.—Behavior of *E. minikyanos*: Four individuals were observed in 1986 but only one collected. The sightings occurred on successive days and led to the

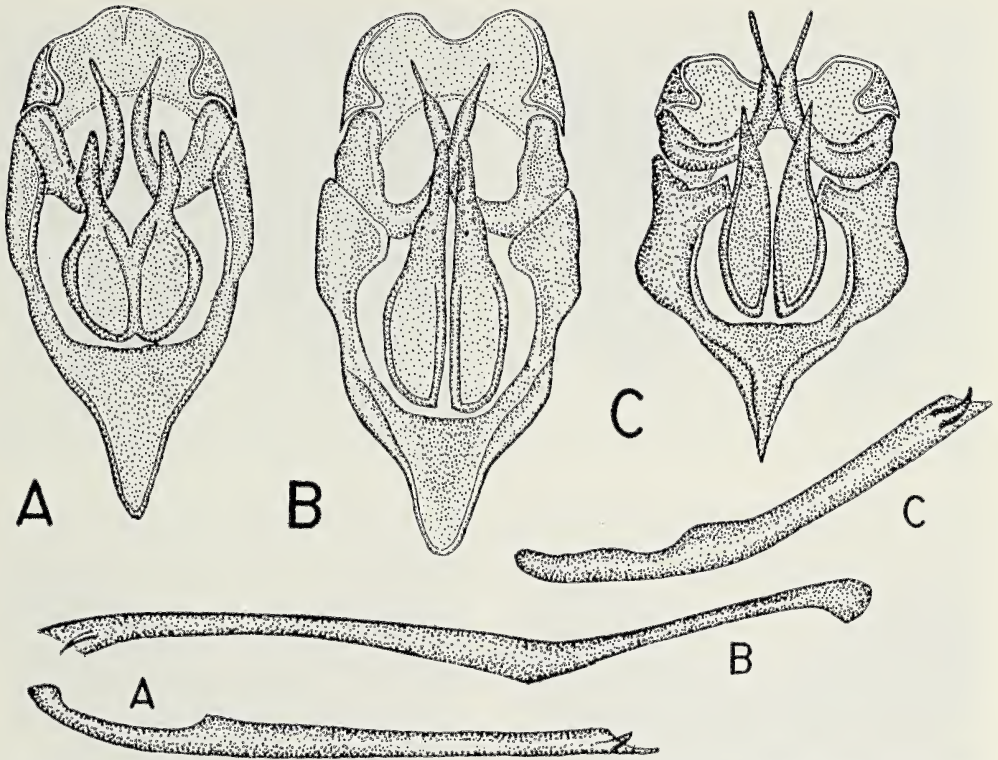


Fig. 2.—LYCAENIDAE. Genitalia of *Electrostrymon*. A–C, male, ventral view with aedeagus removed and placed below (corresponding smaller letters). A. Holotype, *E. minikyanos*. B. *E. angelia boyeri* of Fig. 1. C. *E. pan* of Fig. 1.

increased vigilance necessary to eventually capture the holotype. Individuals observed appeared suddenly from rapid flight to nectar on flowers in a rather xeric clearing of middle Abejas. In contrast to the behavior of *Strymon andrewi* (see below), none returned to a nectar source after being disturbed. The species was not seen in 1987. However, our observation of plant growth and general abundance of certain butterflies suggested that 1987 activity was about two weeks later than that during 1986.

Species status of *E. minikyanos*: No other *Electrostrymon* species or small hairstreak butterfly resembles *E. minikyanos* in wing or genitalic facies. The only other *Electrostrymon* with any blue or violet hue to the upper surface is the female of *E. angelia dowi* (Clench) of the Bahamas. Among Antillean *Electrostrymon*, which *sensu* Riley (1975) appear to be paraphyletic (*E. pan*, at least, being distinctive), *E. minikyanos* does share with *E. angelia* (Fig. 2B) and other “brown” *Electrostrymon* (Riley, 1975, plate 12) the distended condition of the vinculum caudad the saccus. Divergence of facies in *E. minikyanos* is further evidence of probable polyphyly in the Antillean “*Electrostrymon*” as conventionally arranged.

Review: Supplementing general review acknowledged herein, A. Schwartz examined the genitalia of the holotype. Johnson specializes in Theclinae, and he, MacPherson, and Ingraham (1986) have listed taxa examined including dissection of males and females of 359 Nearctic and Neotropical species of 58 genera of the

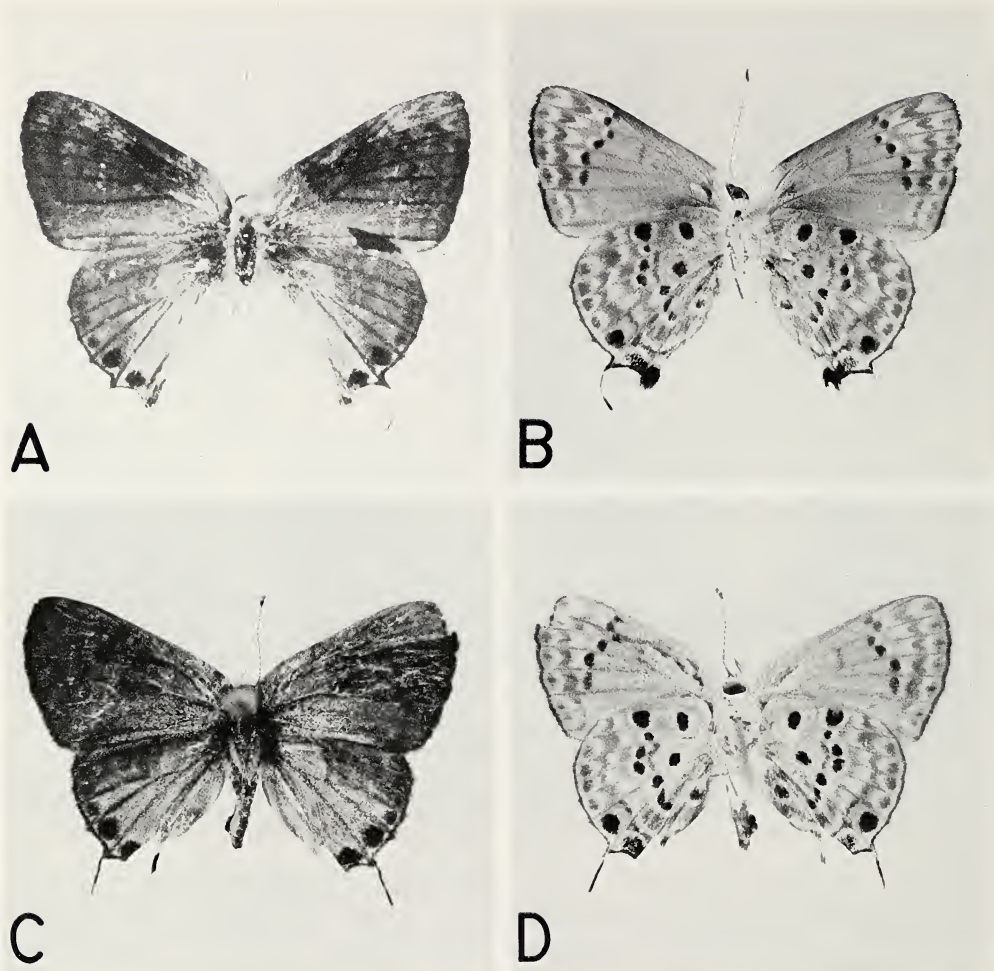


Fig. 3.—LYCAENIDAE. Adults of *Strymon andrewi*. A. Upper surface, holotype male. B. Lower surface, same. C. Upper surface, allotype female. D. Lower surface, same.

eumaeine Theclinae (including 45 species of *Strymon sens. lat.* and *Electrostrymon*). These have served, hereafter, as a basis for Material Examined.

Etymology.—The name combines the Greek prefix *miny* (“small”) and *kyanos* (“blue”), referring to the appearance of the species.

Material examined.—In addition to the material listed in Johnson, MacPherson, and Ingraham (1986), we have been able to compare *E. minikyanos* with the extensive Antillean material of Comstock and Huntington (AMNH) and Clench (CMNH) along with Hispaniolan specimens of Luis Marion Heredia (Santo Domingo, Dominican Republic). Dissections were examined of males and females of the Antillean congeners and comprise AMNH/HS #60, 61 [*E. pan*, data Fig. 1F]; #62, 63 [*E. angelia*, Santiago, Cuba]; #64, 65 [*E. a. boyeri*, data Fig. 1E]; #66, 67 [*E. a. dowi*, Staniard Creek, Andros, Bahamas]; #68, 69 [*E. dominicana*, data Fig. 1C]; #70, 71 [*E. angerona*, data Fig. 1D]; #135, 136 [*E. endymion*, Pichanal, Salta, Argentina; Caldez, Colombia].

Genus *Strymon* Huebner

The unique specimens of *Strymon* captured by us in upland broadleaf forests and adjacent pine woodlands of the Sierra de Baoruco require preliminary com-

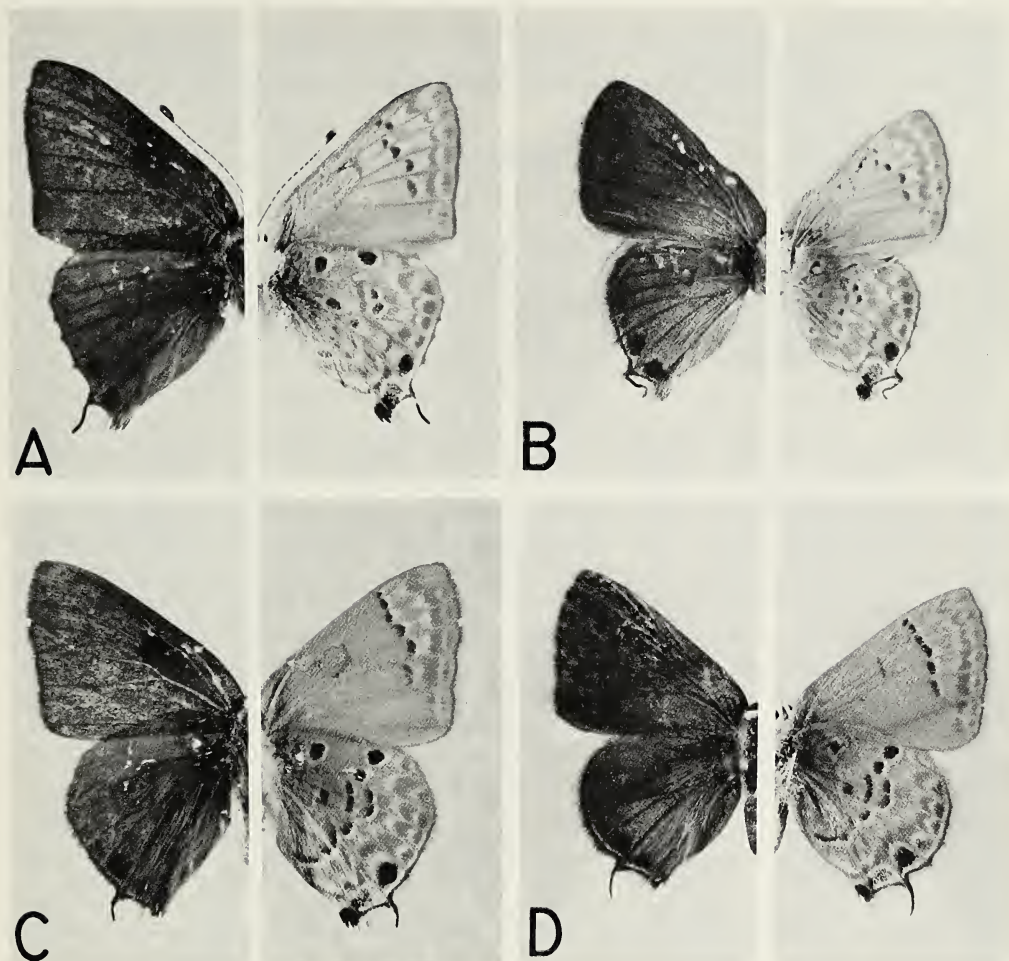


Fig. 4.—LYCAENIDAE. Adults of *Strymon* congeners. Upper surface (left), lower surface (right). A. Holotype male, *S. toussainti*, Fond Parisien, Haiti, 11–18 February 1922. B. Paratype female, *S. toussainti*, same data as entry A. C. *S. columella cybira*, male, Fond Parisien, Haiti, 11–18 February 1922 (AMNH). D. *S. columella cybira*, female, San Cristobal, Dominican Republic, 29 January 1961, leg. B. Heineman (AMNH).

ment. It is easy to characterize the population but more difficult to determine taxonomic status. Although having unique characters, the population also exhibits characters of two relatives, the polytypic, pan-Caribbean *S. columella* (Fabricius) and the Hispaniolan endemic *S. toussainti* Comstock and Huntington. The latter two species are sympatric lowland xerophiles. Neither is known from upland habitats of the Sierra de Baoruco. It is possible that the Las Abejas population represents an undifferentiated descendant of populations ancestral to *S. columella* and *S. toussainti*. Despite the intermediate nature of some characters, it is unlikely that this population represents a subspecies of either *S. columella* or *S. toussainti*, because of unique character combinations and the widespread sympatry of *S. columella* with various endemic Antillean *Strymon*. In addition, it seems unlikely that the population reflects conspecificity of those species, because *S. columella* is consistently distinct from endemic congeners, including *S. toussainti*, through-

out the Antilles. Until someone can substantiate taxonomic and biogeographic reasons warranting an omnibus Antillean *Strymon columella*, with allopatric and sympatric subspecies, we have no choice but to treat the upland pine forest Sierra de Baoruco *Strymon* as follows.

Strymon andrewi, new species

Fig. 3A–D, 5A–C, F

Diagnosis.—In the field this species greatly resembles the blue butterfly *Hemiargus ammon* (Lucas) but has a tail! From other hairstreaks, *S. andrewi* is distinctive in having fresh specimens of both sexes bright blue above. This structural coloration (Fig. 3A, C; 5A, B) is brighter than other “blue-above” Antillean *S. limenia* (Hewitson) and *S. christophei* (Comstock & Huntington). Contrasting these two species, however, the under surface of *S. andrewi* is like that characterizing *S. columella cybira* (Hewitson) [Hispaniolan ssp.] (Fig. 4A, C) and *S. toussainti* [Hispaniolan endemic] (Fig. 4A, B), except that the pattern is more spotted and pronounced than on either of those species. Not only does *S. andrewi* have prominent costo-medial hindwing spots like *S. toussainti* (Fig. 4A, B), large spots, cells CuA2 and 2A, are also directed toward the anal margin, where *S. toussainti*’s pattern is mostly obsolescent. The centro-medial spots of the median line in *S. andrewi* are boldly red (as in *S. christophei*), not black. In both sexes *S. andrewi* has prominent marginal spots extending costad on the hindwing; *S. columella* and *S. toussainti* have these spots limited to cells directly adjacent the tail and anal lobe. Fig. 5C, F shows the genitalia of *S. andrewi*, Fig. 5D, E, G, H those of *S. toussainti* and *S. c. cybira*. Comments on their differences are included below. At Las Abejas, *S. andrewi* was taken at 1530–1750 m in mountain crest pine forest and along its margin with mesic broadleaf forest.

Description.—*Male.* Upper surface of the wings: forewing ground color, black to grayish black, blue basad (Fig. 5A); black androconial brand at distal edge of discal cell. Hindwing ground color, distally silvery blue, basally darker blue to blackish (Fig. 5A). Lower surface of the wings: ground color, gray-white with variegated gray. Forewing with postmedian line of emphatic black dots, costa to vein 2A, dark slash at end of discal cell and bright white chevrons in the margin and submargin. Hindwing with medial band of seven equally large spots and a darkened slash at end of discal cell just basad this line (first spot black, next four red, last two black). Postbasal area with three large black spots—costad, centrad and in anal area, all boldly ringed with white. Submargin and margin with bright white chevrons. Margin with a black line encircling dark gray marginal spots in each cell interspace; *Thecla*-spot emphatically orange; anal lobe and adjacent cell black. Length of forewing: 11.0 mm. *Female.* Upper surface of wings: similar to male but more silvery blue (Fig. 5B) and lacking androconial brand. Lower surface of the wings: similar to male. Length of forewing: 11.0 mm. *Male genitalia.* Fig. 5C. More similar to *S. columella* (Fig. 5D) than *S. toussainti* (Fig. 5E), with the former and *S. andrewi* having saccus distally inclined, strong ventral recurvature of the aedaeagal terminus, and diminutive brush organs. *S. andrewi* differs from *S. columella* by having an extremely thin vinculum and falces, and widely separated lobes on the labides. *Female genitalia.* Fig. 5F. Resembling *S. columella* (Fig. 5H) most, with a wide, cephalically spiral-shaped ductus. The spiral in *S. andrewi* is smaller, however, and more caudally located. The juncture of the ductus bursae with the cervix bursae exhibits the largest sclerotized hood (*sensu* Johnson, 1976) of any of the species. The ductus bursae of *S. toussainti* (Fig. 5G) is relatively constricted and diminutive.

Types.—Holotype male, upper Abejas 1750 m, 8 km on footpath, Las Abejas transect, NW of Aceitillar, Pedernales Province, Dominican Republic, nectaring in sunlight 1330 hrs, July 16, 1986, leg. D. Matusik; allotype female, same data but 1400 hrs, July 17, 1986, both deposited AMNH (AMNH/HS #83, 84). Paratypes: AMNH—(male) same data as holotype but 1300 hrs, 1530 m in xeric pine/broadleaf margin, nectaring in sunlit opening, July 17, 1986, leg. D. Matusik

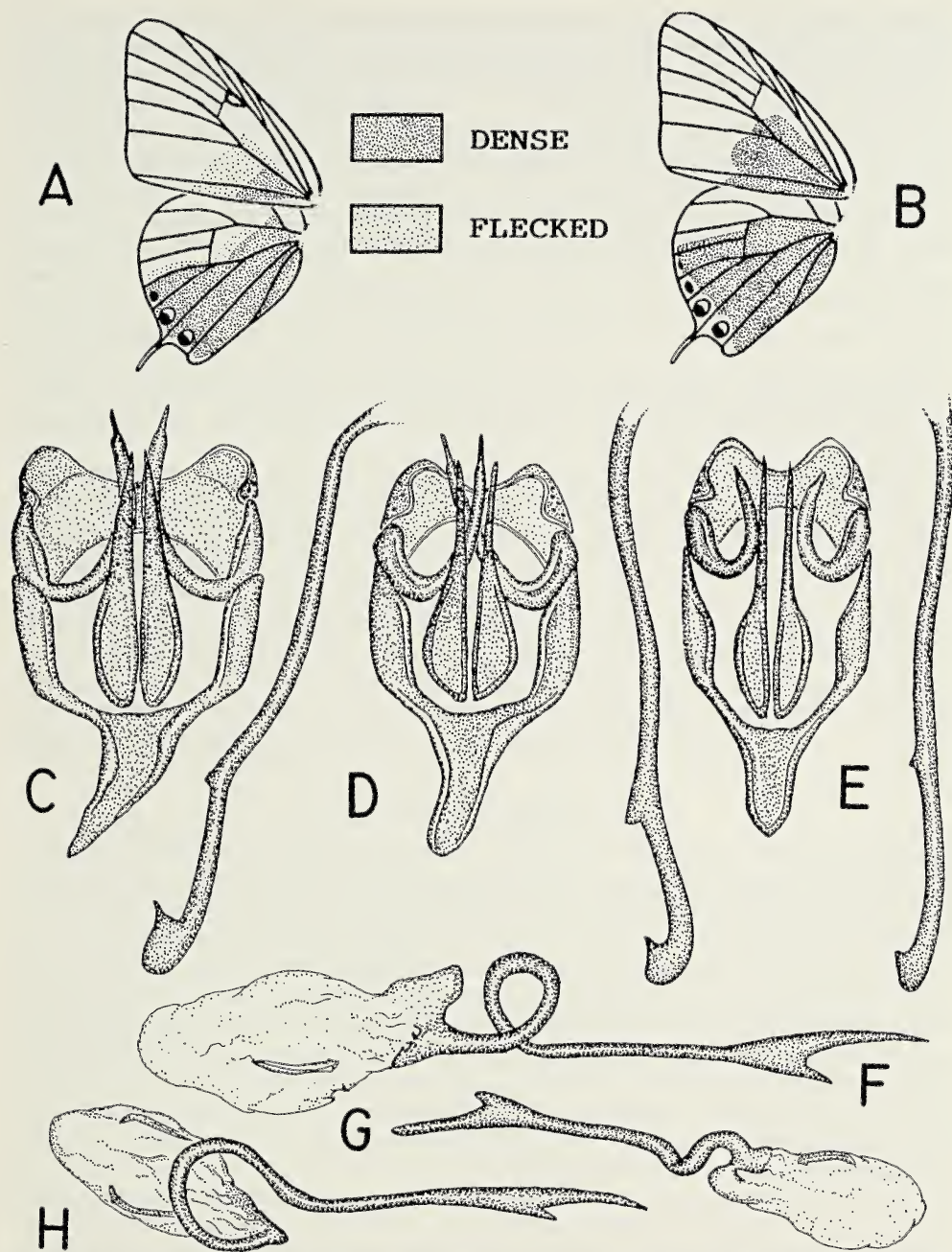


Fig. 5.—LYCAENIDAE. Upper surface structural coloration in *S. andrewi* and genitalia of Hispaniolan *Strymon*. A, B. Extent of upper surface iridescent blue scaling on fresh specimens of *S. andrewi*. A. Male. B. Female. C–E. Male genitalia: left, ventral view of genitalia with aedeagus removed; right, aedeagus, lateral view. C. Holotype, *S. andrewi*. D. *S. c. cybira* of Fig. 4. E. Holotype, *S. toussainti*. F–H. Female genitalia: lateral view of genitalia. F. Allotype, *S. andrewi*. G. Allotype, *S. toussainti*. H. *S. c. cybira* of Fig. 4.

(AMNH/HS #85); (female) same data as paratype male, July 17, 1986, leg. K. Johnson (AMNH/HS #86); (male) upland pine forest, slope from mountain crest, 1780 m, 6 km on footpath, Las Abejas transect, NW of Aceitillar, nectaring on blackberry in sunlight, 1400 hrs, July 17, 1986; (female) data as previous entry but 1520 m, 1430 hrs; (two females) 12 km NW Aceitillar, near Las Abejas, margin with pine forest, 1130 m, July 3, 1984, July 5, 1985, leg. D. Matusik. CMNH—(female) pine forest 1 km NE of Aceitillar, 1430 m, July 17, 1987, leg. K. Johnson; (two males, one female) same locality as primary types, July 15, 1987, leg. K. Johnson; (male) CMNH Expedition Base Camp, 1730 m, circa 4 km from upper Abejas, in xeric pine forest, nectaring on blackberry, July 16, 1987. DMC—(five males, one female) pine forest between 1987 base camp and upper Abejas, July 11–15, 1987, leg. D. Matusik; AME—(two females), same locality as primary types, but July 16, 1987, leg. K. Johnson (on lifetime loan to A. Schwartz). ASC—(two males) 1 km N Aceitillar, 1270 m, December 27, 1986, leg. J. Escobio; (male) 26 km NE Cabo Rojo, Pedernales Province, 800 m, January 2, 1987, leg. A. Schwartz.

Remarks.—Behavior of *S. andrewi*: The species has been observed from numerous captures in 1986 and 1987. Typical of these has been quick flight which, if closely observed, flashes the blue upper surface. Thus, *S. andrewi* is easily construed as a large blue, and could be mistaken in the field for a female of *Hemiargus ammon*. The latter species has not been taken on Hispaniola but *Leptotes cassius* (Cramer) and *Hemiargus thomasi* Clench are frequent upland xerophiles at Las Abejas. These species share the same fabaceous nectar sources which also serve the blues as larval hosts. In contrast to the blues, *S. andrewi* has also been taken on blackberry and other flowers at Las Abejas. Like most hair-streaks, *S. andrewi* rubs its hindwings while at rest, but it also opens its wings regularly, flashing bright silvery-blue. This behavior, larger size and presence of a tail distinguish it at once from other sympatric Polyommatainae.

Species status of *S. andrewi*: Comstock and Huntington (1944) differentiated *S. toussainti* from sympatric *S. c. cybira*. Both are lowland xerophiles (Schwartz, in press) although *S. c. cybira* is more widely distributed on Hispaniola than *S. toussainti* (Schwartz, in press). Placing *andrewi* in trinomial combination with either *S. toussainti* or *S. columella* is not reasonable if both of these species occur on the island and there are no characters to arbitrate which of the two species *S. andrewi* resembles most. Considering the range of distinct wing markings in *S. columella*, *S. toussainti*, *S. limenia*, *S. christophei* and *S. andrewi* (the latter three having distinct structural coloration on wing upper surfaces), the only alternative to considering *S. andrewi* a full species is to return to the pre-1944 view that the entire assemblage is conspecific. Such a view was rejected by Comstock and Huntington (1944) because of the pattern of Antillean sympatry among *C. columella* subspecies and local endemics.

Variation in *S. andrewi* specimens: Preserved specimens of *S. andrewi*, *S. columella* and *S. toussainti* differ distinctively in the way wear affects wing pattern appearance (see Riley, 1975, plates 11, 12). On wing lower surfaces, worn specimens of *S. andrewi* retain both the bold, black-spotted medial bands (traditionally considered characteristic of *S. columella*) and the emphatic basal spots (considered characteristic of *S. toussainti*). Worn specimens of *S. toussainti* retain bold basal spots, but usually have medial spots only costad of the discal cell. The marked upper surface blue in both sexes of *S. andrewi* (flashed in flight and while at rest) is outstanding in fresh specimens, dulls with wear, but is still apparent on worn

specimens. *S. columella*, with females sometimes basally blue when fresh, appears mostly brown in collections. *S. toussainti*, vaguely blue (if at all) when fresh, also appears generally brown in collections with females often showing a lighter brown upper surface suffusion (Fig. 4B).

Review: Aside from general review acknowledged herein, A. Schwartz provided his specimens *S. andrewi* for study and examined the dissections of the primary types. Lee D. and Jacqueline Miller compared photographs of *S. andrewi* to the Antillean *Strymon* at AME. We referred to the genitalic preparations listed in Johnson, MacPherson and Ingraham (1986) and the material examined listed below.

Etymology.—This species is named for the father, the late Andrew Matusik, of the junior author.

Material examined.—Along with material listed in Johnson, MacPherson and Ingraham (1986) we have been able to compare our series of *S. andrewi* to the Comstock and Huntington types of *S. toussainti* (AMNH, CMNH) and *C. christophei* (AMNH), *S. columella arecibo* (AMNH), the types of *Thecla cybira* and *T. limenia* (BMNH), and other specimens of *Strymon* at the AMNH and CMNH. We have also been able to compare *S. andrewi* with hairstreaks collected by Luis Marion Heredia of Santo Domingo and specimens in the collection of A. Schwartz. The type series, as indicated, has been dissected and the dissections are attached in microvials to the individual specimens deposited as noted under TYPES. Representative dissections of various Antillean congeners comprise AMNH/HS #87, 88 [*S. columella arecibo*, holotype male, Guayanilla, Puerto Rico, July 22, 1944; allotype female, Arecibo, Puerto Rico, July 30–August 1, 1941]; #89, 90 [*S. c. cybira*, Fond Parisien, Haiti, February 11–18, 1922; San Cristobal, Dominican Republic, January 29, 1961, B. Heineman]; #91, 92 [*S. toussainti*, holotype male (Fig. 5E), allotype female (Fig. 5G), Fond Parisien, Haiti, February 11–18, 1922, paratype male, Port-au-Prince, Haiti, March 5–11, 1922]; #93, #94 [*S. limenia*, Fond Parisien, Haiti, February 11–18, 1922]; #95, 96 [*S. christophei*, holotype male, Port-au-Prince, Haiti, February 1–6, 1922, allotype female, Paradis, Dominican Republic, 1800 ft, August 15, 1952, leg. W. M. Bush]. There is a single non-paratype of *S. andrewi* from the Sierra de Baoruco near the Haitian border: .6 km SE Los Arroyos, 1200 m, July 3, 1983, leg. A. Schwartz (ASC).

Genus *Heterosmaitia* Clench

Clench (1964) erected this genus to contain the notable Jamaican endemic *bourkei* Kaye. In discussion Clench suggested several mainland congeners for *Heterosmaitia*. Some of these (particularly *Thecla brescia* Hewitson) differ little in morphology from the type of *Rekoa* Kaye (type species *Papilio meton* Cramer). Later, Clench (1970) placed *Heterosmaitia* as a synonym of *Thereus* Huebner (type species *Papilio lausus* Cramer) based on examination of a single male specimen (CMNH) identified by Clench as *T. lausus*. The extant syntype of *P. lausus* (BMNH) is a female. I have examined and dissected this specimen and designated it the lectotype (Fig. 7E); the lectotype's continuous, fluted, genital structure in no way resembles that of *H. bourkei* (Johnson, in press). The battered CMNH male identified as *T. lausus* by Clench is also of questionable identification. Its genitalia differ from numerous BMNH and Milwaukee Public Museum specimens which can be positively identified as *T. lausus* (probably because common usage of "*T. lausus*" actually includes a group of species). Since neither *Heterosmaitia* or *Rekoa* has been revised, we retain *Heterosmaitia*: its type species is *bourkei* and, although Bridges (1988) placed *bourkei* with *Rekoa* in his clerical work, it is not certain that current common usage of *Rekoa* for Antillean and mainland butterflies represents a monophyletic group.

In 1986 we collected hairstreak females at Las Abejas which were difficult to identify. They slightly resembled *Allosmaitia fidena* (Hewitson), but differed from Riley's (1975) description of this Hispaniolan endemic. Like Cuban *A. coelebs*

(Herrich-Schaeffer), they had two hindwing tails (see Riley, 1975, plate 11, p. 99). We also considered if such specimens might represent the then unknown female of *Strymon monopeteinus* Schwartz and Miller (1985). As Schwartz and Miller (1985, pp. 1–2) mentioned, a number of Antillean hairstreaks have similar lower surface patterns, making differentiation of some taxa at first confusing. However, in 1987 we collected a male with the odd lower surface pattern seen the year before and it was apparent from the large forewing scent brand (lack of which is a generic character of *Allosmaitia*) that we had been dealing all along with an undescribed species. Further examination of these specimens indicates they constitute a sister species of *H. bourkei* which we describe below.

Heterosmaitia abeja, new species

Fig. 6A–D, 7A, D

Diagnosis.—Similar only to *H. bourkei* of Jamaica, (*A. fidena* of Hispaniola has no male scent brand, and along with differing wing pattern (see below) females of *H. abeja* have three black marginal spots on the hindwing upper surface in cells CuA2 to M3 lacking in *A. fidena*). Differing from *H. bourkei* (Fig. 6E, F) as follows: *H. abeja* males—(a) under surface with submarginal black lines greatly reduced (bold in *H. bourkei*); (b) lower surface hindwing with medial black band rather straight (inclined baso-costad in *H. bourkei*), with line detached from yellow *Thecla*-spot (conjoined in *H. bourkei*) and generally rounded toward anal angle (incised and jagged in *H. bourkei*); and (d) anal area darkly suffused black and bluish (*H. bourkei* with conspicuous second yellow spot along anal lobe); *H. abeja* females—(a) with all differences of male (though less vividly marked) (b) three black marginal spots extending from the anal lobe to cell M3 on the hindwing upper surface (*H. bourkei* with continuous black marginal line somewhat enlarged or blotch-like at these veins). Of less certain significance, but notable—forewing expanse in the known specimens of *H. abeja* (\bar{x} of primary types, 11.75 mm) smaller than eleven specimens of *H. bourkei* examined by us (males \bar{x} = 14.2, range 13.5–15.0 mm; females \bar{x} = 16.0, range 15.0–18.0 mm) and the male scent brand on the holotype of *H. abeja* is shiny gray, not black as in all *H. bourkei* examined. Genitalic differences are reviewed below.

Description.—*Male*. Upper surface of wings: ground color iridescent azure blue, forewing base to postmedian area, margins and apex blackish; hindwing, anal margin to costal vein of discal cell iridescent azure blue, margins and costal areas blackish. Forewing with shiny parabolic scent brand distad in discal cell. Single long black tail, terminus vein CuA2. Lower surface of wings: ground color, light gray; forewing with slight submarginal darker line, vaguely apparent and dark continuous postmedian line costa to cell CuA1, in latter slightly inclined basad; hindwing with submarginal line vague to obsolescent, postmedian line, continuous and generally vertical across wing from costa to slightly basad the yellow *Thecla*-spot, then bent roundly toward anal margin; area of anal lobe suffused darkly bluish and black. Length of forewing: 12.0 mm (holotype). *Female*. Upper surface of wings: ground color, dull silvery blue (forewing base to postmedian area, hindwing base to costal area and margins) marginal areas fuscous. Forewing without scent brand; hindwing with three prominent black marginal spots, cells CuA2 to M3. Lower surface of wings: as on males but less vividly marked and with slight yellow apparent in the area of the anal lobe. Length of forewing: 11.5 mm (allotype). *Male genitalia*. Fig. 7A. Similar to *H. bourkei* (Fig. 7B) but (a) valvae more elongate relative to vincular configuration, (b) prong for brush organ attachment reduced and (c) ratio of aedeagus length to caudal length of vincular arc 3.3 (*H. abeja*), 2.6 (*H. bourkei*), with caecum of *H. abeja* not inclined laterally as on *H. bourkei* (see Clench, 1964, fig. 6). *Female genitalia*. Fig. 7D. Similar to *H. bourkei* (Fig. 7C): ductus bursae with two disjunct sclerotized elements (caudad and cephalad a central transparent juncture), cephalic element slightly displaced distally. *H. abeja* differing slightly, with (i) caudal element of ductus bursae more basally constricted, (ii) cephalic component of ductus bursae less displaced laterally and (iii) corpus bursae comparatively small with two large, pronged, signa.

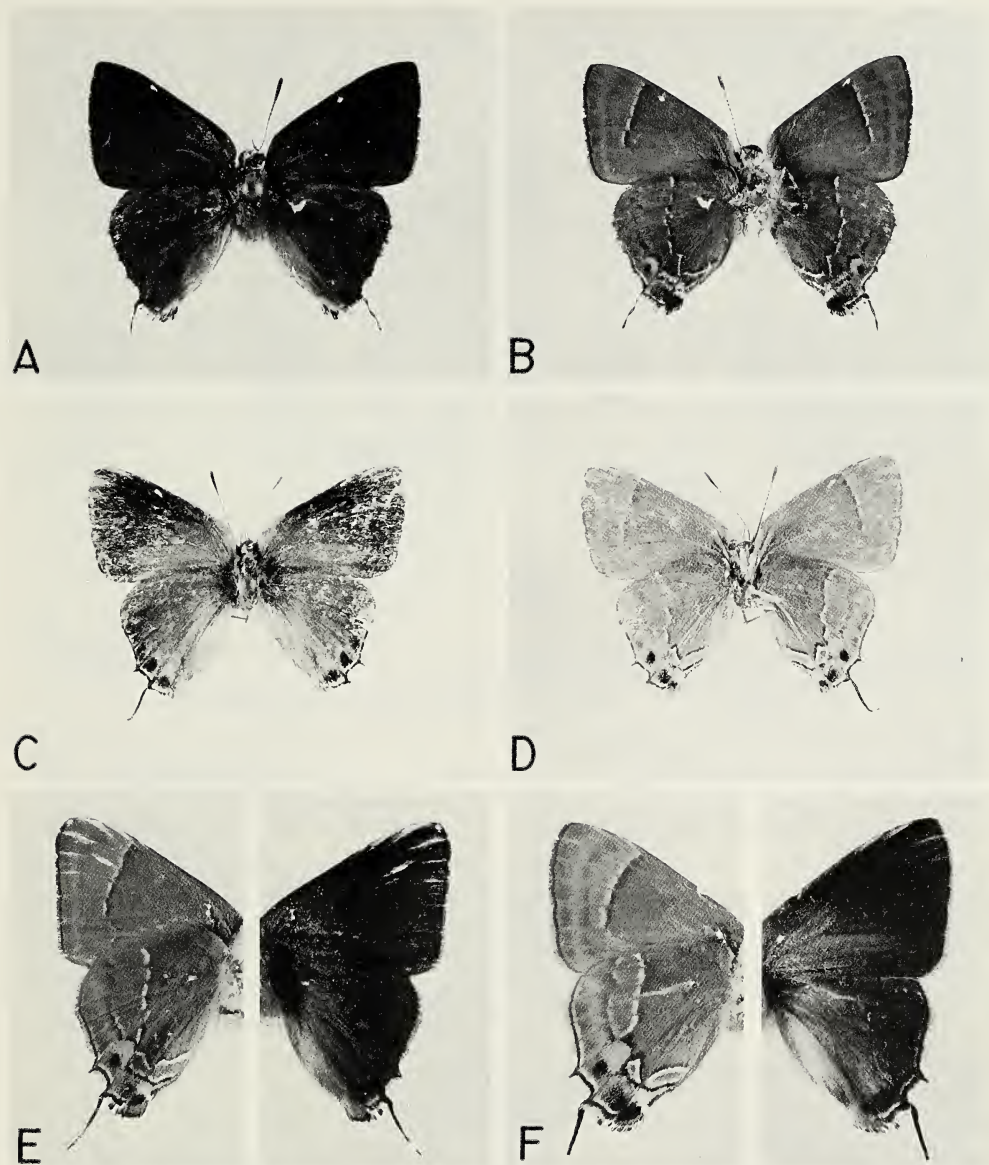


Fig. 6. —LYCAENIDAE. Adults of *Heterosmaitia abeja* and *H. bourkei*. A. Upper surface, holotype male, *H. abeja*. B. Lower surface, same. C. Upper surface, allotype female, *H. abeja*. D. Lower surface, same. E. Upper surface (right), lower surface (left), *H. bourkei*, male, Duncans, Trelawny Parish, 28 October 1984 (AMNH). F. Same, *H. bourkei*, female, same data.

Types. —Holotype male, upper Abejas, nectaring in sunlight on blackberry, 15 July 1987, leg. Kurt Johnson, deposited CMNH; allotype female, same location, same conditions, 10 July 1986, leg. Kurt Johnson, deposited CMNH (AMNH/HS #104, 105 transferred to CMNH).

Remarks. —Behavior of *H. abeja*: The collecting conditions of this species are interesting because nearly all hairstreaks taken at Las Abejas, including *A. fdena*,

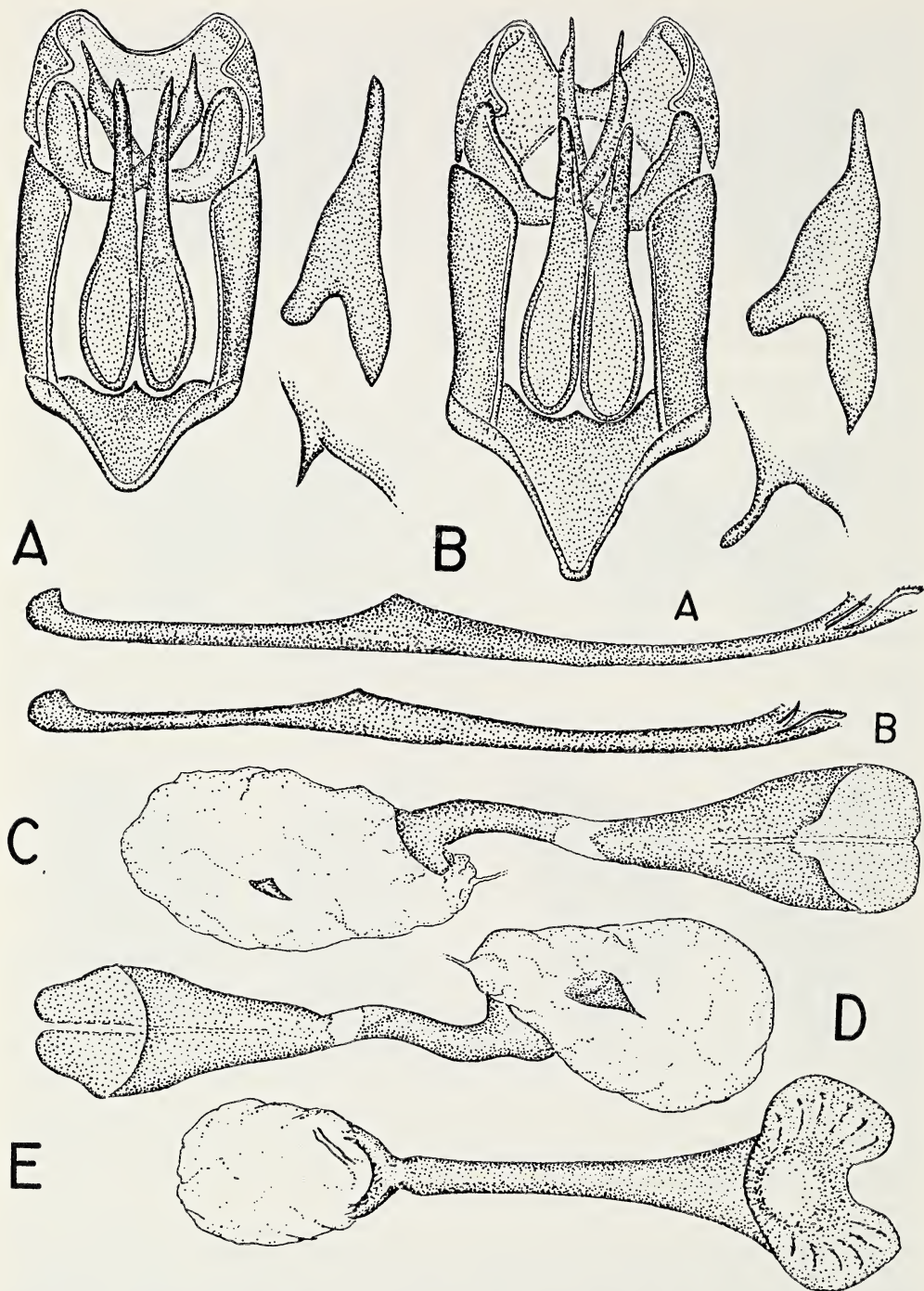


Fig. 7.—LYCAENIDAE. Genitalia of *Heterosmaitia*. A, B. Male genitalia: left, ventral view of genitalia with aedeagus removed; right (above), lateral view, valve; right (below), lateral view vincular spur for attachment of brush organ. Below (with smaller letters), lateral view, aedeagus. A. Holotype, *H. abeja*. B. *H. bourkei* of Fig. 6. C, D. Female genitalia, lateral view. C. *H. bourkei* of Fig. 6. D. Allotype, *H.*

S. andrewi, *T. azia* and *S. monopeteinus*, have been captured on three blackberry bushes which, because of their location near the margin with pine forest, are exposed to morning sunlight from as early as 0900 hrs. Both specimens of *H. abeja* were collected here but neither was seen in flight. Like other theclines at the site, they have been collected by sporadic checking of these bushes for nectaring butterflies. Standing at these bushes all day has never proved a useful way to collect. On certain days no theclines appear. Another visitor of these bushes is the infrequently collected skipper *Epargyreus spanna* (Johnson and Matusik, 1986). In one instance, on the same flower clump, Johnson had to choose between netting *E. spanna* or an additional specimen of *S. andrewi*.

Species status of *H. abeja*: Given distinctive characters and geographic occurrence of this butterfly, its specific status appears certain (see below).

Biogeography: Distributions of *H. abeja* and *H. bourkei* represent a disjunction of two congeners endemic to montane areas of the southern paleoisland of Hispaniola and Jamaica, respectively. This may reflect a tectonic relationship between the two regions as long term adjacent elements on the northern edge of the Caribbean plate (Sykes et al., 1982; Williams, 1986). Miller and Miller (in press) and Johnson (1981 and ms.) suggest certain vicariant patterns in the origin of the Caribbean butterfly fauna. Description of *H. abeja* adds an interesting element to this discussion. Discovery of a *Heterosmaitia* species in Hispaniola requires mention of the original description of *Thecla bourkei* Kaye (1925). Kaye originally described the species from a specimen with Trinidad data, but later (1931) changed the type locality to Jamaica after the species had been collected often there but never subsequently authenticated from Trinidad. This change has never been questioned by lepidopterists, but is worthy of mention with the appearance of a related taxon on Hispaniola.

Etymology.—We have given this species the name of the Las Abejas region, using the singular form to conform to vernacular usage and the feminine gender of the generic name.

Material examined.—We compared the types of *H. abeja* to eleven specimens and dissections of *H. bourkei* (all AMNH) from Duncans, Trelawny Parish, Jamaica, October 24, 1984 (one male, one female); October 28, 1984 (one male, one female), January 20, 1984 (two males, two females) (comprising AMNH/HS #137, 138, 139, 140); Islington, St. Anns, Jamaica, February 20, 1951, leg. B. Heineman (male); Rio Bueno, St. Ann's, Jamaica, December 30, 1952 (female); Sandy Quilly, St. Andrews, Jamaica, December 3, 1951 (female).

Genus *Terra*, New Genus

Fig. 8A–D, 9B, 10

Preliminary comment.—This new genus is currently being revised by Johnson. It includes, along with a number of mainland species, a new species from Hispaniola which cannot be placed in any known eumaeine genus. Thus, to allow treatment of new Hispaniolan taxa as a group, and to make the new generic name available for colleagues, it is described here.

Terra (which, along with a number of undescribed species, contains the species *tera* Hewitson, *cana* Hayward, *chilica* Schaus, *calchinia* Hewitson and *hycarra* Hewitson [all originally described in "*Thecla*"]) is the immediate sister genus of

←

abeja. E. Lectotype female, *Papilio lausus* Cramer, Utitl. Kapellen, (1775–90 [1779]), 3(20): 70, pl. 233, f E, BMNH Cramer syntype, labelled "Surinam," "designated lectotype by K. Johnson, 1988."

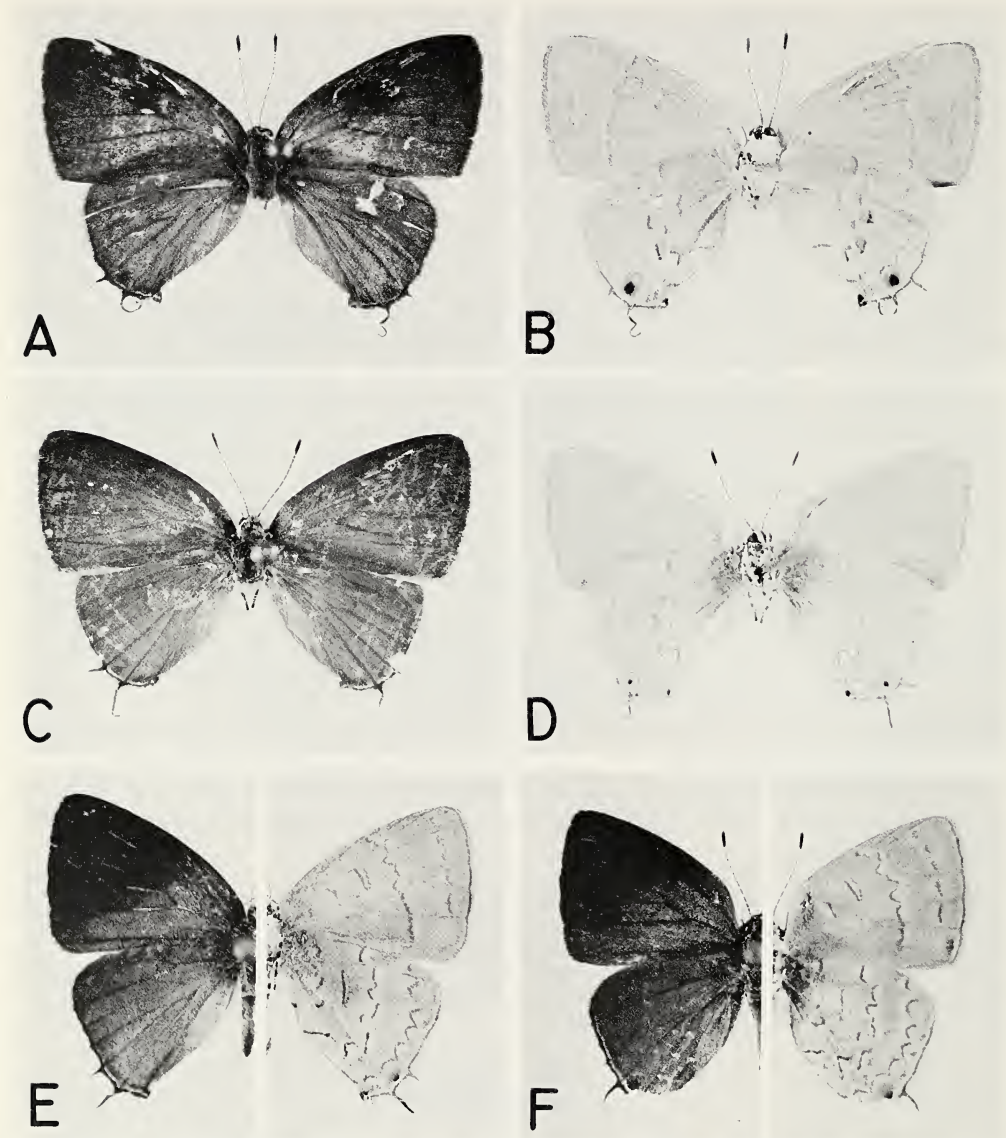


Fig. 8.—LYCAENIDAE. Adults of *Terra* and *Nesiostrymon*. A. Upper surface, holotype male, *T. hispaniola*. B. Lower surface, same. C. Upper surface, allotype female, *T. hispaniola*. D. Lower surface, same. E. Upper surface (left), lower surface (right) male, *N. celida*, lower Abejas, July 6, 1986, leg. Kurt Johnson. F. Same, female, *N. celida*, same data.

Nesiostrymon Clench (1964) (species *celida* Lucas, *shoumatoffi* Comstock & Huntington, and *celona* Hewitson [also all originally described in "*Thecla*"]]). *Nesiostrymon* also contains a number of undescribed mainland species. In a four taxon statement, *Terra* and *Nesiostrymon* form the apotypic sister lineage to respective plesiotypic outgroups summarized here as the *Thecla uzza* Hewitson assemblage and the *Thecla celmus* Cramer assemblage (Fig. 10).

The familiar small blue Antillean hairstreaks, species *celida* and *shoumatoffi*

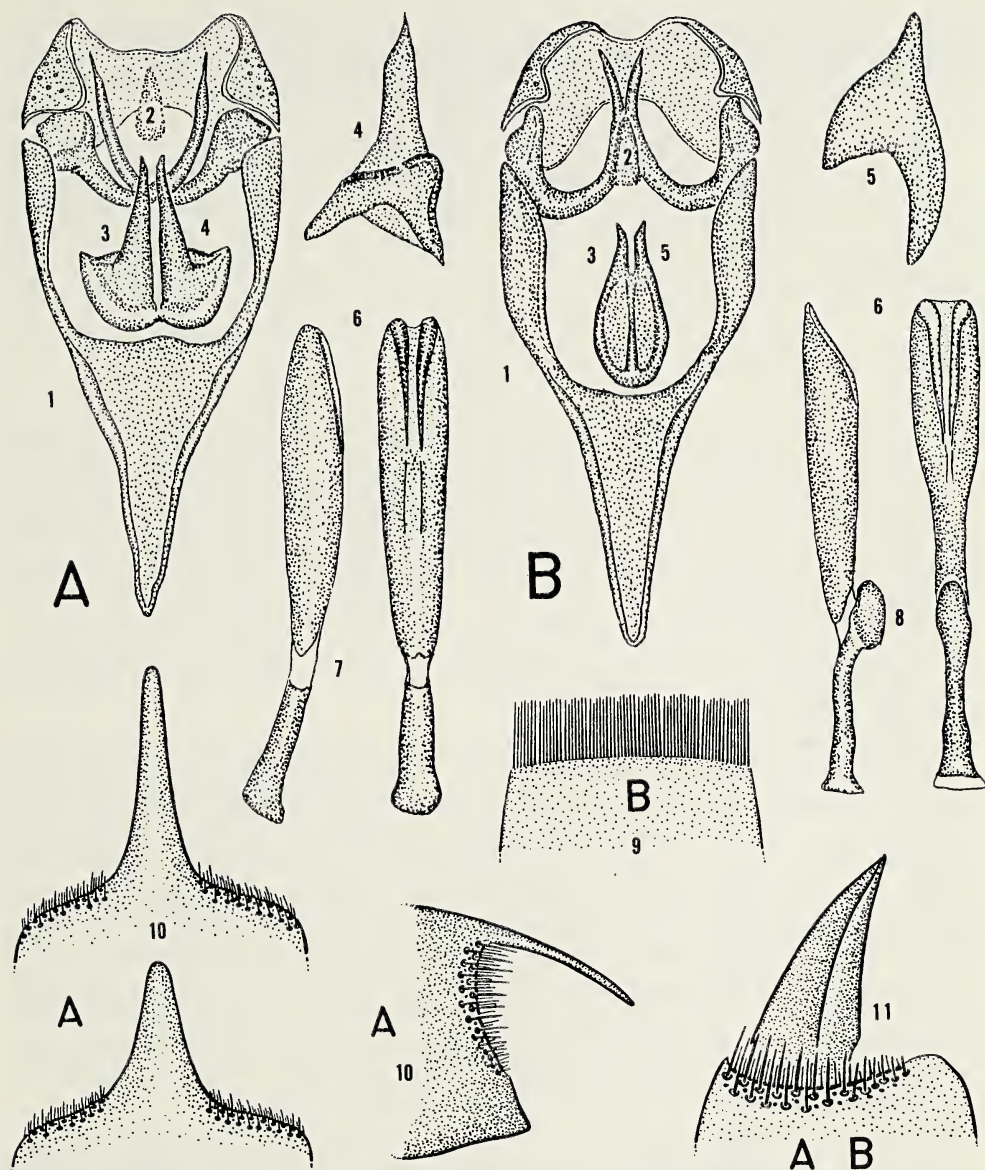


Fig. 9.—LYCAENIDAE. Morphology of *Nesiostrymon* (A) and *Terra* (B). For each of the larger letters A and B, above left: ventral view, genitalia with aedeagus removed; above right: lateral view of valve. Below right: female genitalia, lateral view (left), ventral view (right). Numerals refer to characters listed Table 1. For each of the smaller letters A and B, below: A, far left: dorsal view, incised posterior cavity of eighth tergite with terminal prong, *N. celida celida*, Cuba (above and immediate right), *N. c. ssp.* of Fig. 8 (below). B, right center: dorsal view, normal eighth tergite, holotype *T. hispaniola*. A, B, below right: lateral view of heavily sclerotized, pointed papillae anales, *Nesiostrymon* and *Terra*.

were placed by Clench (1964) in *Nesiostrymon* as an endemic Antillean genus; Clench suggested that *Thecla tera* might be a mainland relative. However, *Nesiostrymon* taxa differ greatly in morphology from *Thecla tera* with only the former and *Thecla celona* having (a) a specialized incised posterior cavity in the eighth

Table 1.—Character state matrix used for cladogram construction of *Nesiostrymon*, *Terra*, and relatives. Outgroup consists of *Thecla asa*, *T. alda*, *T. carnica*, and *T. emendatus* (from study of their types and other specimens), as well as several undescribed species currently under study. Characters used for Lundberg rooting of parsimonious network specified at bottom.

	Characters														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Nesiostrymon</i>	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1
<i>Terra</i>	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1
<i>Uzza</i> complex	1	1	0	0	0	0	1	1	0	0	0	0	0	1	1
<i>Celmus</i> complex	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lundberg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

tergite of males and (b) a two component genital plate configuration in females (*Terra* species have three). When *Terra* and *Nesiostrymon* are recognized as monophyletic sister groups, both contain mainland and Antillean members while their outgroups occur only on the mainland. The capture at Las Abejas of a sister species of *Thecla tera* necessitated the distinction of *Terra* and *Nesiostrymon*. Dissection of the eventual type series of *T. hispaniola* (which is sympatric with *Nesiostrymon celida*) indicated a normal eighth tergite in males and a three-component genital plate in females. The erection of *Terra* is based on the cladograms (Fig. 10) derived from a cladistic analysis (PAUP: Swofford, 1985) based on characters listed in Table 1.

Diagnosis.—*Nesiostrymon* and *Terra* are small (forewing 10–13.0 mm) hair-streaks, iridescent blue to purplish above. In males, large parabolic scent patches variably overlap fuscous wing apices, and in both sexes the under surface is grayish to white with a pattern composed primarily of a darker rounded medial band and a brilliant *Thecla*-spot. In *Nesiostrymon* (Fig. 8E, F) the hindwing medial band is black; in *Terra* it is yellow, orange or reddish. *Nesiostrymon* males have the eighth tergite specialized to an “subcordate incised posterior cavity” [sensu Field, 1967a, 1967b; Johnson, 1988] with a caudally directed dorsal prong (Fig. 9, A10); *Terra* males have a normal eighth tergite (Fig. 9, B9). *Nesiostrymon* females have two components in the sclerotized genitalic configuration, a lamellar/antrum component separated by an unsclerotized area from a ductal component (Fig. 9, A6, 7); *Terra* females have these components conjoined with a third component, a large sclerotized bulb, occurring at this juncture (Fig. 9, B6, 8).

Description.—**Adult.** Body blackish with finely overlaid gray to bluish hairlike spines; eyes ringed with white; antennae black, finely striped with white. **Male.** Upper surface of wings: ground color dull iridescent blue to violet with margins of hindwing and margins and apices of forewing variously dark fuscous; forewing with parabolic androconial band, usually black and variously intersecting with fuscous distal ground color; hindwing with long tail, terminus vein CuA2, short tail, terminus vein CuA1. Lower surface of wings: ground color ranging from white to dull gray-brown, forewing with postmedian line, disjunct or continuous, usually across entire wing, most often orange, reddish or yellow with darker edges; limbal area with bright yellow, orange or reddish *Thecla*-spot and often with various limbal suffusion. Length of forewing: 12.5–15.0 mm. **Female.** Upper surface of the wings: similar to male but with fuscous marginal areas more extensive and with no forewing androconium. Lower surface of wings: as on males. Length of forewing: 12.5–15.5 mm. **Male tergal morphology and genitalia.** Fig. 9, B2, 3, 5, 9. Eighth tergite unspecialized (B9). Genitalia with (i) vinculum thin and elongately parabolic (B1); (ii) saccus elongate and parabolic (B1); (iii) valvae short (not filling vincular arc, never extending to cephalad arch of falces) and compressed laterally (B5) [in *Nesiostrymon*, Fig. 9, A2, 3, 4, 10, valvae have thick, steeply angled, incised lobes, tapered terminally]; (iv) aedeagus elongate, exceeding in length $2.75 \times$ ventro-caudal length of vincular arc. **Female tergal morphology**

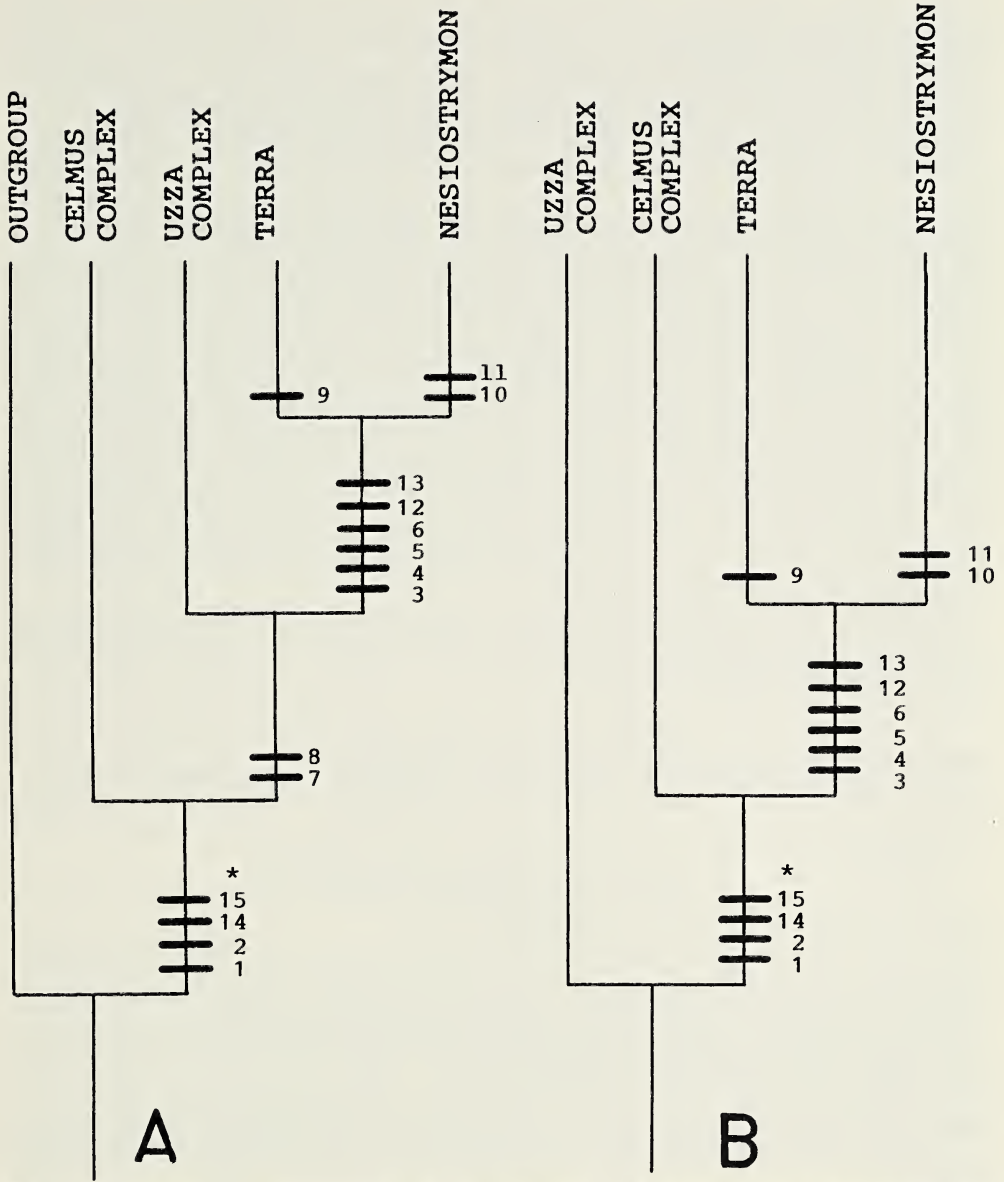


Fig. 10.—Cladograms of *Nesiostrymon*, *Terra*, and relatives. A. Cladogram derived from parsimonious distribution of unweighted characters and rooted using an outgroup as described in text (Consistency Index = .923). Uniquely derived apomorphies are specified by horizontal bars on internodes, and represent characters as numbered in text. Characters 1, 2, 14, and 15 were polarized using information provided by Johnson on additional taxa not included in the outgroup. B. As in Fig. 10A, cladogram rooted using the Lundberg method based on the presumed primitive states listed at the bottom of Table 1 (Consistency Index = .889).

and genitalia. Fig. 9, B6, 8, 11. Eighth tergite unspecialized but papillae anales distinctively sclerotized into pointed configuration [shared with *Nesiostrymon* but not outgroups] (Fig. 9, A11, B11). Genitalia with (i) sclerotized lamellal/antrum configuration conjoined to ductus with a large sclerotized ventral bulb (Fig. 9, B9) [in *Nesiostrymon*, Fig. 9, A6, 7 there are two sclerotized components separated by a clear, unsclerotized area]; (ii) corpus bursae with two small pronglike signa [as on *Nesiostrymon*].

Type species. — *Thecla tera* Hewitson (Ill. diurn. Lep. Lycaenidae, 1863–78 [1878], 1: 211; 2: pl 84, f 714, 715).

Distribution. — Primarily mainland (*T. tera*, *T. chilica*, *T. cana*, *T. hycarra*, *T. calchinia*) but with one species occurring on Hispaniola described herein.

Remarks. — Phylogenetic analysis of *Terra* and related species: parsimonious distributions of characters (Fig. 10) were constructed using PAUP (Swofford, 1985) based on the following taxa and specimens — *Terra* (based on types and additional specimens); *Nesiostrymon* (based on types and additional specimens); *Thecla uzza* complex (based on types, additional specimens of *T. uzza*, and several undescribed species); and *Thecla celmus* complex (based on types, additional specimens of *T. celmus*, *T. seudiga* Hewitson, *T. jambe* Godman and Salvin, and several undescribed members of this complex). Species criteria were derived from standard taxonomic procedures involving consistent differences in characters of the wings and genitalic and tergal morphology. The monophyly of the group including the above four groups is derived from a survey of the *Thecla* grade of Eumaeini (*sensu* Bridges, 1988) and the taxa listed by Johnson, MacPherson and Ingraham (1986) and Johnson (in press). Consistent with this survey, the outgroup used consisted of *T. asa* Hewitson, *T. alda* Hewitson, *T. carnica* Hewitson, and *T. emendatus* Druce (from study of their types and other specimens), as well as several undescribed species currently under study.

Characters: The following describes the apomorphic state for characters used for constructing cladograms in Fig. 10, as listed in Table 1. Numbers in parentheses refer to numbered structures in Fig. 9.

1. Forewing of male with ellipsoidal androconial brand (*sensu* Eliot, 1973) encompassing distal end of discal cell and basal portion of cells M3, M2, M1 and the radial veins.

2. Lower surface of hindwing with pattern elements occurring (a) medially at least in cells SC + R1, Rs, M1, M2, M3, CuA1, CuA2, and 2A, and (b) postbasally in SC + R1.

3. Male genitalia with width of vincular arc equal to or exceeding 2.5 times the length of saccus.

4. Male genitalia with width of vincular arc less than length of saccus (1).

5. Length of valves not exceeding ventro-caudal length of vincular arc (3).

6. Area caudad of valve apex and basal to arch of falces with a membrane-enfolded, ellipsoidal sclerotized pad (the "extra-valvular element") (2).

7. Female genitalia with clear, non-sclerotized juncture between the caudal and cephalic components (6).

8. Non-sclerotized juncture with prominent, sclerotized, ovate bulb ventrally (the "bulb") (8).

9. "Bulb" located about equidistant from caudal and cephalic ductal termini.

10. Clear, non-sclerotized juncture smooth (uninterrupted by sculpturing or additional components) over its entire circumference (juncture "simple") (7).

11. Eighth tergite of male heavily sclerotized throughout, forming incised posterior cavity of subcordate shape (Field, 1967a, 1967b; Johnson, 1988) with ventro-caudally directed prong (10).

12. Papillae anales of female with heavy lateral sclerotization caudally inclined, forming a pointed terminus (11).

13. Lower surface of hindwing with pattern elements crossing inside discal cell, and occurring either (a) postbasally in at least one of the following cells: cell SC + R1, cell CuA2, cell 2A; or (b) basally in the discal cell.

14. Aedeagus of male with length (measured along lateral surface, including length of caecum displaced outside the plane of aedeagal shaft) equal to or exceeding 2.75 times the ventro-caudal length of vincular arc.

15. Male genitalia with ventro-caudal length of vincular arc equal to or less than saccus length (1).

Plesiomorphic states for the apomorphic characters described above are readily inferred except for 1, 2, 9 and 13 (entries 2 and 13 describe surface wing patterns in particular, site-specific, terms). Concerning these: (1) outgroups generally lack androconia or, in a few taxa, exhibit a small, concentrated, androconial mark limited to occurrence basad the crossvein of the forewing discal cell; (2) outgroups

all have more elaborate patterns including (a) distally expansive, continuous or lunular, median bands, (b) extensive markings in the postbasal area and (c) pronounced limbal markings in addition to the usual *Thecla*-spot and accordant ground color suffusions; (9) there is one undescribed outgroup in which a “bulb”-shaped element occurs at the cephalic base of the ductus bursae, abutting the distal end of the corpus bursae; (13) outgroup pattern is as in Characters, entry 2.

Taxonomic status of *Terra*: The above analysis indicates *Terra* and *Nesiostrymon* form a monophyletic group distinguished from their immediate outgroups (the “*Thecla uzza*” and “*Thecla celmus*” complexes) by six synapomorphies of the wings, genitalia, and terminal abdominal morphology (Table 1: Characters 1, 3–6, and 13). The monophyly of *Terra* and *Nesiostrymon* is supported by autapomorphies of the genitalia and tergal morphology (Table 1: Characters 9, 11, and 12). High consistency values (Fig. 10) for cladograms result from the various, very distinctive, morphological characters which separate these taxa (e.g., the incised posterior cavity of the eighth male tergite, distribution of microtrichia, etc.). “Outgroup” and “outstate” rootings (Fig. 10A, B, respectively) give identical results concerning the monophyly of *Terra* and *Nesiostrymon*. We anticipate that further revisionary research will resolve relations in the “*Thecla*” taxa included in the outgroups. We recognize *Nesiostrymon* and *Terra* as genera for three reasons: their respective species diversities, the distinct hiatus between their major apomorphic structural characters, and the congruence of their geographic distributions. These indicate two distinct evolutionary lineages whose current patterns of diversity and spatial distribution result from the action of similar historical events on two ancient, and widespread, ancestral populations.

Etymology.—The name, considered feminine, is Latin referring to “land” and signifies, in contrast to *Nesiostrymon*, the basically mainland distribution of the genus.

Terra hispaniola, new species

Fig. 8A–D, 9B

Diagnosis.—The only *Terra* species from the Antilles, differing from sympatric *Nesiostrymon celida* (Fig. 8E, F) in both sexes by the yellow hindwing band (black in *N. celida*) and dull blue-violet upper surface ground color (brilliant azure blue in *N. celida*). In addition, upper surface forewing in females is fully blue in *T. hispaniola* except for the margins, black from margin to subapex in *N. celida*. The species differs morphologically as in generic treatment, and *T. hispaniola* is distinctive from mainland *Terra* species as noted in Remarks below.

Description.—*Male*. Upper surface of wings: ground color dull violet blue, margins and apices cloudy black; forewing with large parabolic androconial band emphatic over ground color; hindwing with long tail, terminus vein CuA2, short tail, terminus vein CuA1. Lower surface of wing: ground color dirty white, forewing with gray, suffused postmedian line, costa to cell CuA1; hindwing with medial band of broken yellow patches slightly suffused with black, limbal area gray-white with slight cloudy suffusion, *Thecla*-spot light yellow, blackened centrad. Length of forewing: 13.0 mm (holotype). *Female*. Upper surface of wing: similar to male but with fuscous marginal areas more extensive and without forewing androconia. Lower surface of wings: as on males. Length of forewing: 12.5 mm (allotype). *Male genitalia*. Fig. 9B. Differing from mainland congeners in the parabolically tapered shape of the valval ventrum (congeners have ovate to squarish bilobed configurations and abruptly tapering caudal extensions). *Female genitalia*. Fig. 9B (right, center). Differing from mainland congeners in compact configuration of the cephalic and caudal components of the ductus bursae. Congeners have both components more elongate, particularly the cephalic component on some mainland species has

length 15–20 × width (*T. hispaniola* circa 6–7 × width). In *T. hispaniola* the ventro-central sclerotized “bulb” is located flush with the terminus of the cephalic ductal component (in congeners it is often semi-detached from the ductus on a thin stalk).

Types. — Holotype male and allotype female (a mating pair) taken slightly below upper Abejas, 6 July 1986, leg. K. Johnson, both deposited CMNH (AMNH/HS #106, 107, transferred to CMNH). Paratypes: DMC—(male) same locality as primary types, 5 July 1984, leg. D. Matusik (AMNH/HS #108 transferred to DMC). AME—(male) upper Abejas, patrolling path, 13 July 1987, leg. K. Johnson, on lifetime loan to Albert Schwartz (AMNH/HS #109 transferred to AME). AMNH—(male) same location as primary types, nectaring on small blue flowers in sunlight, 15 July 1987, leg. K. Johnson (AMNH/HS #110).

Remarks. — Behavior of *T. hispaniola*: All specimens have been taken in a relatively restricted area of Las Abejas, just below upper Abejas, where mesic broadleaf forest largely replaces pine forest. However, this area is still much drier than middle or lower Abejas and has numerous open areas where many xerophilic insects and plants are found. This habitat has produced a different moth fauna than lower and middle Abejas (J. E. Rawlins, personal communication). All individuals of *T. hispaniola* have been taken while patrolling close (0.3 m) above ground or nectaring on flowers of about the same height. However, on 16 July 1987, an individual was observed near the base camp (see entry under *Panoquina*, Hesperiniinae) a xeric area nearly 3 km from upper Abejas. All collection habitats of *T. hispaniola* differ markedly from those of *N. celida*. We have found *N. celida* only in the vicinity of lower Abejas and most commonly in dense woods or along their immediate margins.

Species status of T. hispaniola: The trans-Caribbean disjunction of the *T. hispaniola* distribution and its unique characters support its status as a distinct species.

Review: In addition to general review acknowledged in this paper, A. Schwartz examined a paratype male and the genitalia of the primary types.

Etymology. — This species is named for the island of Hispaniola.

Material examined. — We consulted the material listed in Johnson, MacPherson and Ingraham (1986) and in addition the dissections prepared for the revision of *Nesiostrymon* and *Terra* (along with their outgroups). These included (i) the types of *Thecla celona*, *T. tera*, *T. dicaea* Hewitson, *T. hycarra*, *T. celmus*, *T. calchinia*, *T. asa*, *T. phrutus* (Geyer), *T. emandatus*, *T. alda*, *T. carnica*, *T. uzza*, *T. heraldica* Dyar, *T. hicetas* Godman and Salvin, *T. jambe*, *T. hesychia* Godman and Salvin (all BMNH), *T. shoumatoffi*, *T. celida aibonito* (both AMNH); (ii) innumerable specimens of all taxa included in *Nesiostrymon*, *Terra* and groups listed above [these specimens and dissections from AMNH, CMNH, BMNH, AME, Museum National d'Histoire Naturelle (Paris), Field Museum of Natural History, and Milwaukee Public Museum]; and (iii) a series of 70 specimens of *N. celida* from lower Abejas collected 1984–1987 (AMNH, CMNH, DMC).

Polyommatainae

Genus *Leptotes* Scudder

In 1987, after discovering a large population of *Calisto chrysaoros* Bates deep within the densely wooded bottomland of lower Abejas, intensive collections were made in this habitat for further specimens. In previous years we had considered this area too inaccessible to collect, since there is hardly room among the heavy plant cover to maneuver a collecting net. To our surprise a single male polyommataine was captured here which proved to be a new species. Hitherto, we had never collected a “blue” within the moist bottoms of Las Abejas. Rather, all other blues from the vicinity, in our experience and Schwartz’ (A. Schwartz, personal

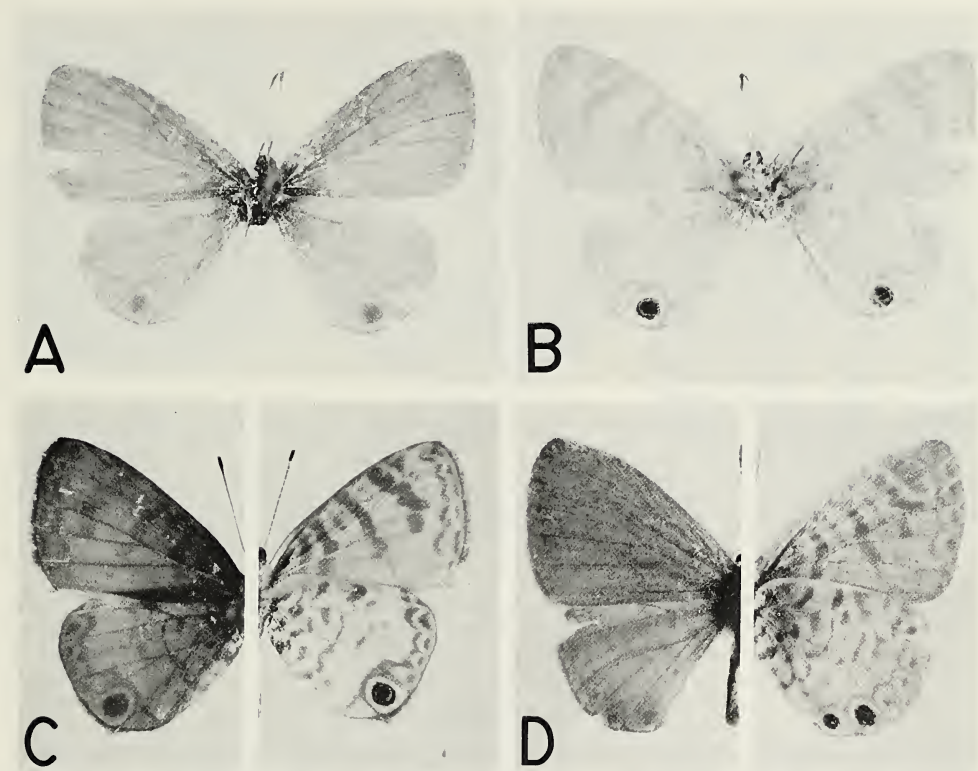


Fig. 11.—LYCAENIDAE. Adults of Antillean *Leptotes*. A. Upper surface, holotype male, *L. idealus*. B. Lower surface, same. C. Upper surface (left), lower surface (right), *L. perkinsae* Faraway, Stony Hill, St. Andrews, Jamaica, 2 February 1955, leg. B. Heineman (AMNH). D. same, *L. cassius*, 3 km E upper Abejas, pine forest, 15 July 1987, leg. D. Matusik (AMNH).

communication) are upland xerophiles occurring in pine forest above 1250 m and invading Las Abejas only along its upland pine forest margin (see *L. cassius*, Fig. 11D).

Leptotes idealus, new species

Fig. 11A, B; 12C

Diagnosis.—Similar only to *L. perkinsae* of Jamaica in having a single, large, black anal spot in cell CuA2 of the hindwing under surface. Differing from *L. perkinsae* (Fig. 11C) in being pale purplish brown on the upper surface (not washed with vivid blue iridescence) and on the under surface having (a) forewing stripes restricted costad, particularly the medial stripe which occurs costad only (in *L. perkinsae* emphatic and disjunctly broken into costad and caudad components, latter filling at least cells CuA1 and CuA2) and (b) anal spot and marginal spots of cells CuA1 and M3 generally in same plane (not greatly expansive outside rest of spot line as in *L. perkinsae*). Male genitalia of *L. idealus* with four terminal spines only (inner spine greatly elongate), on a constricted valval terminus (Fig. 12C), not (a) a lobate terminus with a single inner pointing spine as on *L. cassius* (Fig. 12A) or (b) with four terminal spines and an elongate, upward pointing fifth spine on the inner valval margin as on *L. perkinsae* (Fig. 12B).

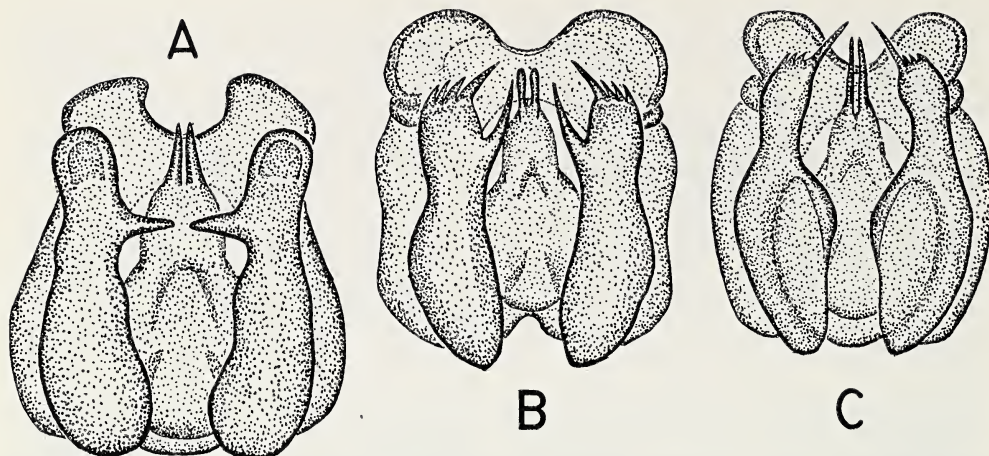


Fig. 12.—LYCAENIDAE. Genitalia of Antillean *Leptotes*. Male genitalia, ventral view with aedeagus in place. A. *L. cassius* of Fig. 11. B. *L. perkinsae* of Fig. 11. C. holotype, *L. idealus*.

Description.—*Male*. Upper surface of wings: both wings with ground color pale purplish brown, margins lighter tawny. Hindwing with large black spot at cell CuA2 showing through from lower surface. Lower surface of wings: ground color, shiny white; forewing with concentric vertical brown bands, basal, medial and postmedial, not extending caudad beyond caudal vein of discal cell; hindwing with concentric brown lines distad toward end of discal cell; rest of wing immaculate except for margin which has large black anal spot at cell CuA2 and light dots in the cell interspaces costad to the margin. *Female*. Unknown. *Male genitalia*. Fig. 12C. Typical of *Leptotes* (Eliot, 1973) but differing from *L. cassius* (Fig. 12A) and *L. perkinsae* (Fig. 12B) markedly in the valvae. *L. idealus* has four terminal valval spines, the inner one being greatly elongate. The valvae are greatly constricted in the terminal one-third and concave on the inner lateral margin toward the base. In *L. cassius*, the valval terminus is widely lobate with a single inward pointing spine; *L. perkinsae* has four terminal spines, the inner one which is greatly elongate and another elongate, upward pointing spine on the inner margin of the terminal lobe.

Types.—Holotype, male, extremely dense moist woods, bottom of Las Abejas, 18 July 1987, 1100 hrs, disturbed into flight in filtered sunlight, leg. K. Johnson, deposited CMNH (AMNH/HS #111 transferred to CMNH).

Remarks.—Behavior of *L. idealus*: This species was caught in densely wooded understory where the only other butterfly species seen was *Calisto chrysaoros* Bates. The eventual *T. idealus* holotype flew up, from an apparent ground level perch, after being disturbed by efforts of the collector to move through adjacent underbrush. This behavior contrasts with that of upland xerophilic blues which flutter in bright sunlight about the blossoms of various Fabaceae. In dense woods at Las Abejas, two other butterfly species, *Nesiostrymon celida* and *Anetia jaegeri*, can also be found flying in areas of filtered sunlight.

Species status of L. idealus: Distinct characters and the distributional disjunction of this species from its apparent sister species *L. perkinsae* (see below) assure its species status.

Biogeography: As noted under the entry and citations concerning *H. abeja*, the disjunct geographic occurrences of *L. perkinsae* and *L. idealus* may reflect the cited tectonic relationship between Jamaica and the southern paleoisland of Hispaniola.

Etymology.—We are pleased to name this species for the Ideal Dominicana S. A. company, Messrs. R. Caceres (President, Santo Domingo), M. Kelly, V. Garcia

and R. Reyes (facility Supervisors 1981–87, Cabo Rojo). Without the logistical assistance of personnel at Cabo Rojo, work at Las Abejas would have been impossible.

Material examined.—We have been able to compare the type of *L. idealus* to specimens of *L. cassius* taken by us at many Dominican Republic localities (AMNH, CMNH) and material collected in the Dominican Republic by Luis Marion Heredia (Santo Domingo). We have compared *L. idealus* to the long series of *L. perkinsae* in the B. Heineman collection (AMNH). Dissections of this material include *L. cassius*, 12 km marker, on Ideal Dominicana road to Aceitillar, 500 m, leg. D. Matusik (AMNH/HS #141); pine forest margin above upper Abejas, 15 July 1987, leg. K. Johnson; Florida City, Florida, 9 June 1946 (AMNH/HS #142); Biscayne Bay, Florida (AMNH/HS #143); *L. perkinsae*, Faraway, Stony Hill, St. Andrews, Jamaica, 2 January 1955, B. Heineman (AMNH/HS #144, 145); Claremont, Jamaica, 11 March 1929 (AMNH/HS #146).

Hesperiidae

Undescribed skippers are not unexpected on Hispaniola. The family is often poorly collected by lepidopterists, and a complex taxonomy in many groups has made identification difficult. Recently, Gali (1983) described two new species of *Choranthus* from the southern paleoisland, and Schwartz and Sommer (1986) described a subspecies of *Synapte malitiosa* Herrich-Schaeffer which occurs in the same region. From 1985 to 1987, in pine woodlands surrounding Las Abejas, we captured specimens of a distinctive upland population of *Panoquina* Hemming. This population represents an undescribed taxon.

Hesperiinae

Genus *Panoquina* Hemming

Evans (1955) recognized fifteen species of *Panoquina*, distributed from the United States and southern Canada southward to Argentina. Riley (1975) recorded six species from the Antilles. Hitherto, three species of *Panoquina* have been reported from Hispaniola—*P. ocola* (Edwards), *P. sylvicola* (Herrich-Schaeffer) and *P. nero* (Fabricius). These have been considered easily distinguished by wing characters (Klots, 1951; MacNeill, 1975; Riley, 1975; Scott, 1986) (Fig. 14). From 1985 to 1987 we captured specimens of *Panoquina* near Las Abejas exhibiting characters of both *P. sylvicola* and *P. ocola*. These specimens had an emphatic upper surface spot in the forewing discal cell (traditionally characteristic of *P. sylvicola*), and an obsolescent costally directed line on the hindwing under surface (considered characteristic of *P. ocola*). Subsequent study of genitalia of these and other *Panoquina* species indicated the presence of a distinctive subspecies of *P. ocola* in the Sierra de Baoruco. The study also showed that *P. hecebolus* Scudder occurs on Hispaniola (see Remarks).

Panoquina ocola distipuncta, new subspecies

Fig. 13A–D, 15B, F

Diagnosis.—*P. o. distipuncta* has the white patch on the forewing upper surface (caudo-distad in the discal cell) hitherto considered diagnostic of *P. sylvicola* and *P. hecebolus*. On *P. sylvicola* (Fig. 14B) this marking is large and elongate; in *P. o. ocola* (Fig. 14C) it occurs in very few specimens as a “pinpoint” (Scott, 1986, see Remarks); in *P. hecebolus* (Fig. 14E) and *P. o. distipuncta* it is a round spot of moderate (pinhead) size. On the hindwing under surface *P. o. distipuncta* has a thin, costally directed postmedian white line or spot-row, similar to *P. hecebolus*. This line is usually absent in *P. o. ocola* and occurs as a whitish to bluish-white undersurface hindwing bar (or dense spot row) in *P. sylvicola*. Genitalia, partic-

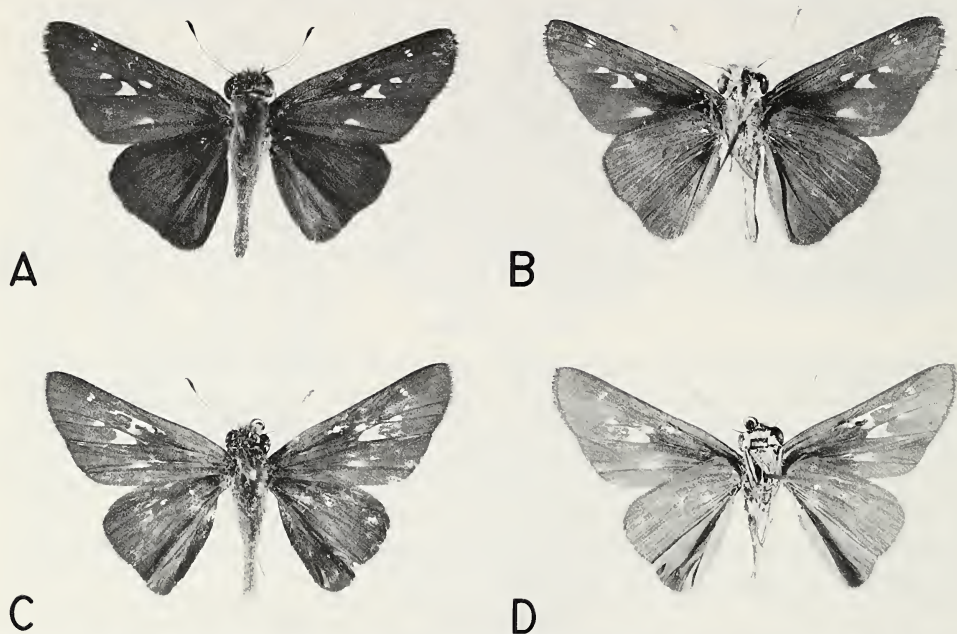


Fig. 13.—HESPERIIDAE. Adults of *Panoquina ocola distipuncta*. A. Upper surface, holotype male. B. Lower surface, same. C. Upper surface, allotype female. D. Lower surface, same.

ularly of females, are diagnostic: the lamella postvaginalis of *P. sylvicola* is prominent, bilobate and densely covered with microtrichia; *P. hecebolus* lacks the microtrichia completely and is broadly concave rather than bilobate (Fig. 15E); *P. o. ocola* (Fig. 15D) has dense microtrichia and a liplike terminal shape which, in *P. o. distipuncta* (Fig. 15F) appears generally larger, and distally more lobate (see Remarks). *P. o. ocola* and *P. sylvicola* are xerophiles generally associated (sometimes as pests) with sugar cane and other agricultural monocots (Riley, 1975). *P. o. distipuncta* occurs in upland pine forest generally remote from areas of domestic planting.

Description.—*Male.*—Upper surface of the wings: ground color brown, forewing with yellow-white patches, often golden-edged, caudo-distad in discal cell, postmedian in cells CuA2, CuA1 and M3, and as four to five apical dots along the radial veins. Hindwing with occasional small white dots in cell CuA1 and M3 as on the lower surface. Lower surface of wing: ground color olive drab, forewing with markings as on upper surface, hindwing with postmedian line of variously emphatic whitish spots, generally suffused in a line from costa to obsolescence toward the anal lobe. Length of forewing: 16 mm (holotype). *Female.* Upper surface of wings: as on males. Lower surface of wings: as on males. Length of forewing: 18 mm (allotype). *Male genitalia.* Fig. 15B. Valvae generally wide from area adjacent vinculum to terminus (valvae of Dominican Republic *P. o. ocola*, Fig. 15A, appearing inclined toward vinculum); harpe with dorsally inclined hook arising ventro-centrally along the valval terminus (a character emphatic in *P. luctuosa* Herrich-Schaeffer of Ecuador) (harpe of Dominican Republic *P. o. ocola* appearing to arise more ventro-distad [see Remarks]). *Female genitalia.* Fig. 16C. Genital terminus with microtrichia forming terminal liplike sclerotizations of the lamellae postvaginalis, this structure not as pronounced as the larger, heavily sclerotized bilobate terminus in *P. sylvicola*. In specimens examined, microtrichial structures of *P. o. distipuncta* (Fig. 16C) appear to form a more expansive terminal structure than of *P. o. ocola* (Fig. 16A). *P. hecebolus* completely lacks terminal microtrichia (Fig. 16B).

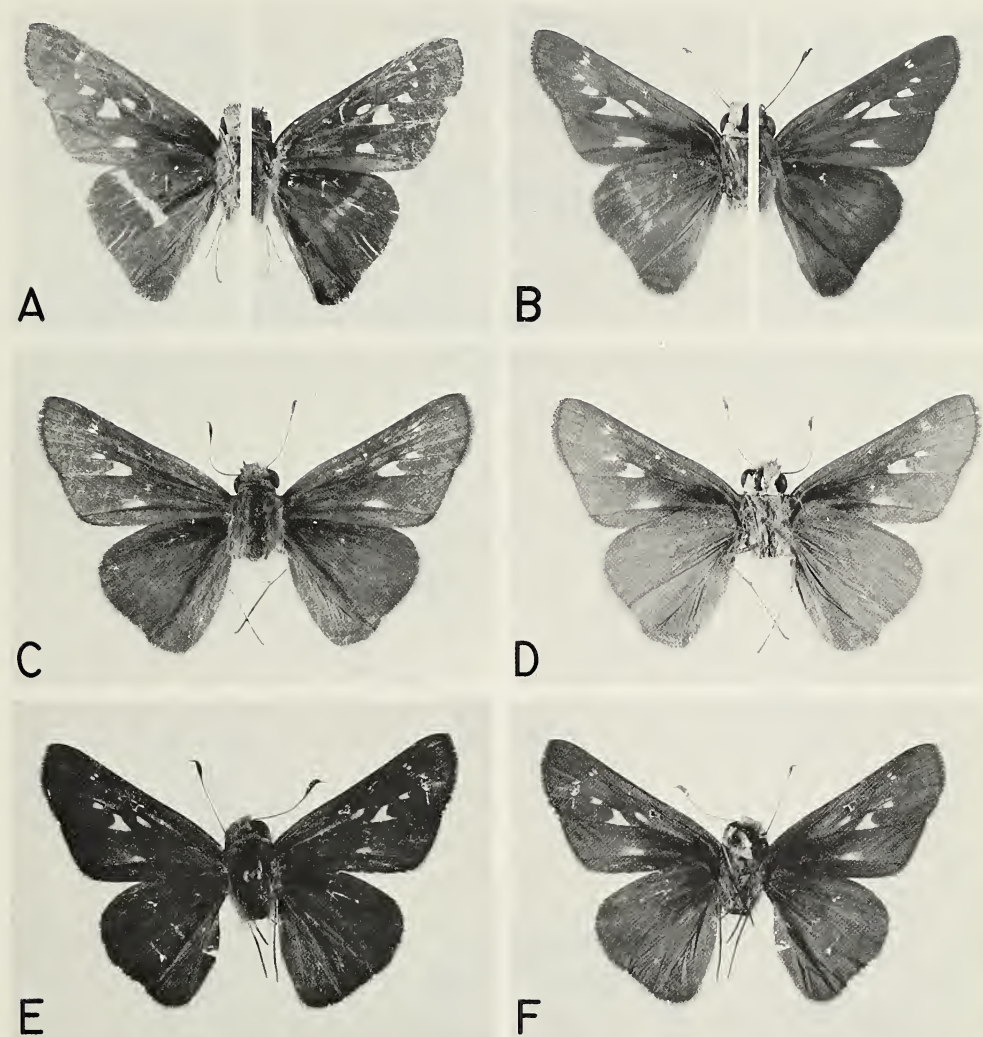


Fig. 14.—HESPERIIDAE. Adults of *Panoquina* congeners. A. Upper surface (right), lower surface (left), *P. nero*, male, Bamboo Hole Canyon, La Vega Province, Dominican Republic, 22 July 1987, leg. Johnson and Matusik (AMNH). B. Upper surface (right), lower surface (left), *P. sylvicola*, male, grassland near Aceitillar, Pedernales Province, Dominican Republic, 14 July 1987, leg. Johnson and Matusik (AMNH). C. Upper surface, *P. ocola ocola*, male, Rio Baiquate bridge, SE Jarabacoa, La Vega Province, Dominican Republic, 24 July 1987, leg. Johnson and Matusik (AMNH). D. Lower surface, same. E. Upper surface, *P. hecebolus*, female, Port-au-Prince, Haiti, 1–6 February 1922 (AMNH). F. Lower surface, same.

Types.—Holotype male, allotype female, 1987 CMNH Expedition Base Camp, 18°10'N, 71°37'W, 1600 m, circa 4 km from upper Abejas, in xeric pine forest, 16 July 1987, leg. K. Johnson, deposited CMNH (AMNH/HS dissections #39, 40 transferred to CMNH). Paratypes: CMNH—(one male, one female) same data as primary types (AMNH/HS #41, 42 transferred to CMNH), (two males), pine forest on way to Las Abejas, 4–11 July 1985 [circa 1520 m], leg. D. Matusik

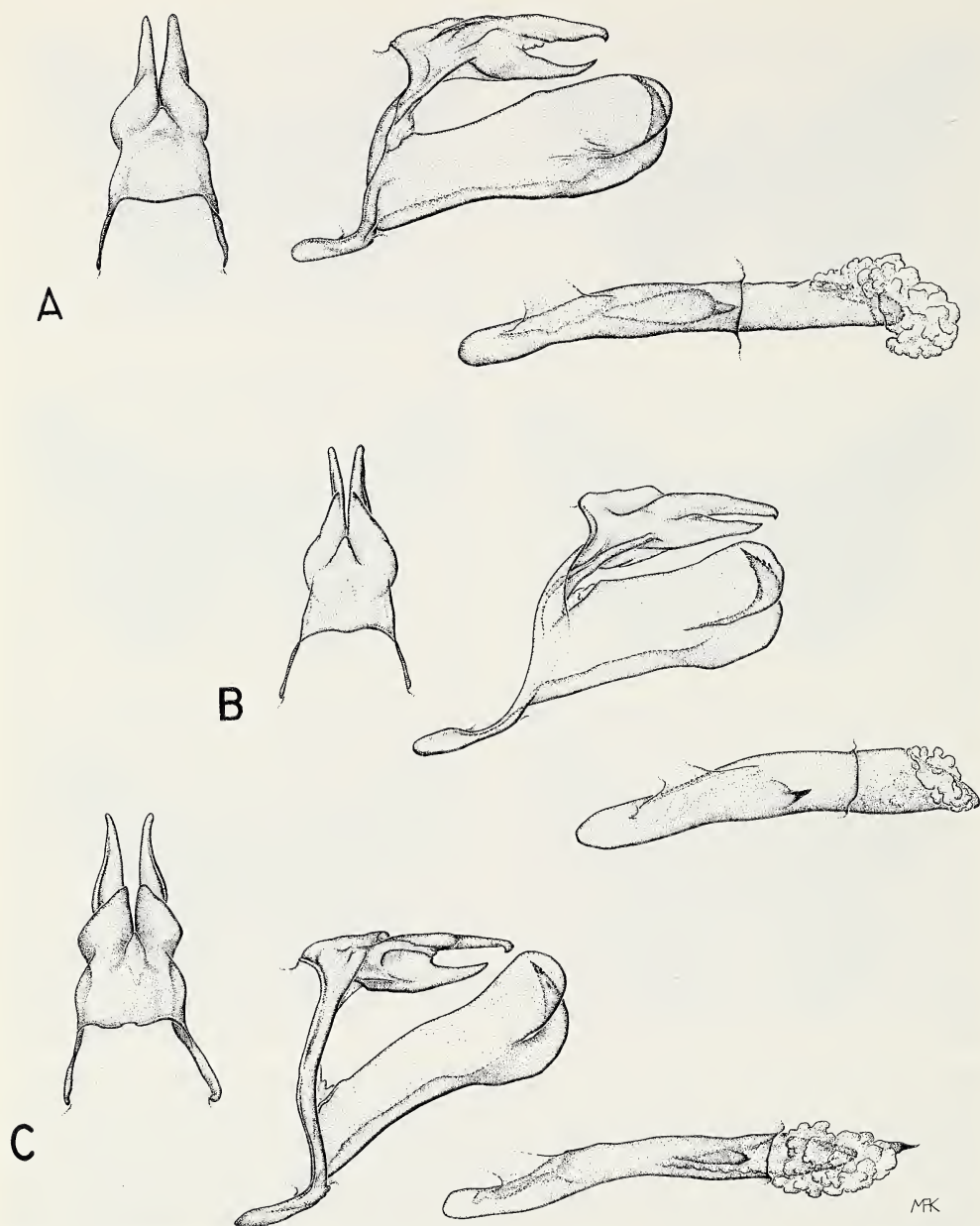


Fig. 15. — HESPERIIDAE. Male genitalia of selected *Panoquina* species. A–C: left, dorsum of tegumen/uncus; center, lateral view of genitalia with aedeagus removed; lower right, aedeagus. A. *P. ocola ocola* of Fig. 14. B. Holotype, *P. ocola distipuncta*. C. *C. hecebolus*, Port-au-Prince, Haiti, 1–6 February 1922 (AMNH).

(AMNH/HS #43, 46 transferred to CMNH); AMNH—(two males, two females) pine forest on way to Las Abejas, July 13, 1986 [circa 1520 m], legs. D. Matusik and K. Johnson (AMNH/HS #49, 50, 51, 52); AME—(two males, one female), data as on primary types, on lifetime loan to A. Schwartz (AMNH/HS #47, 120,

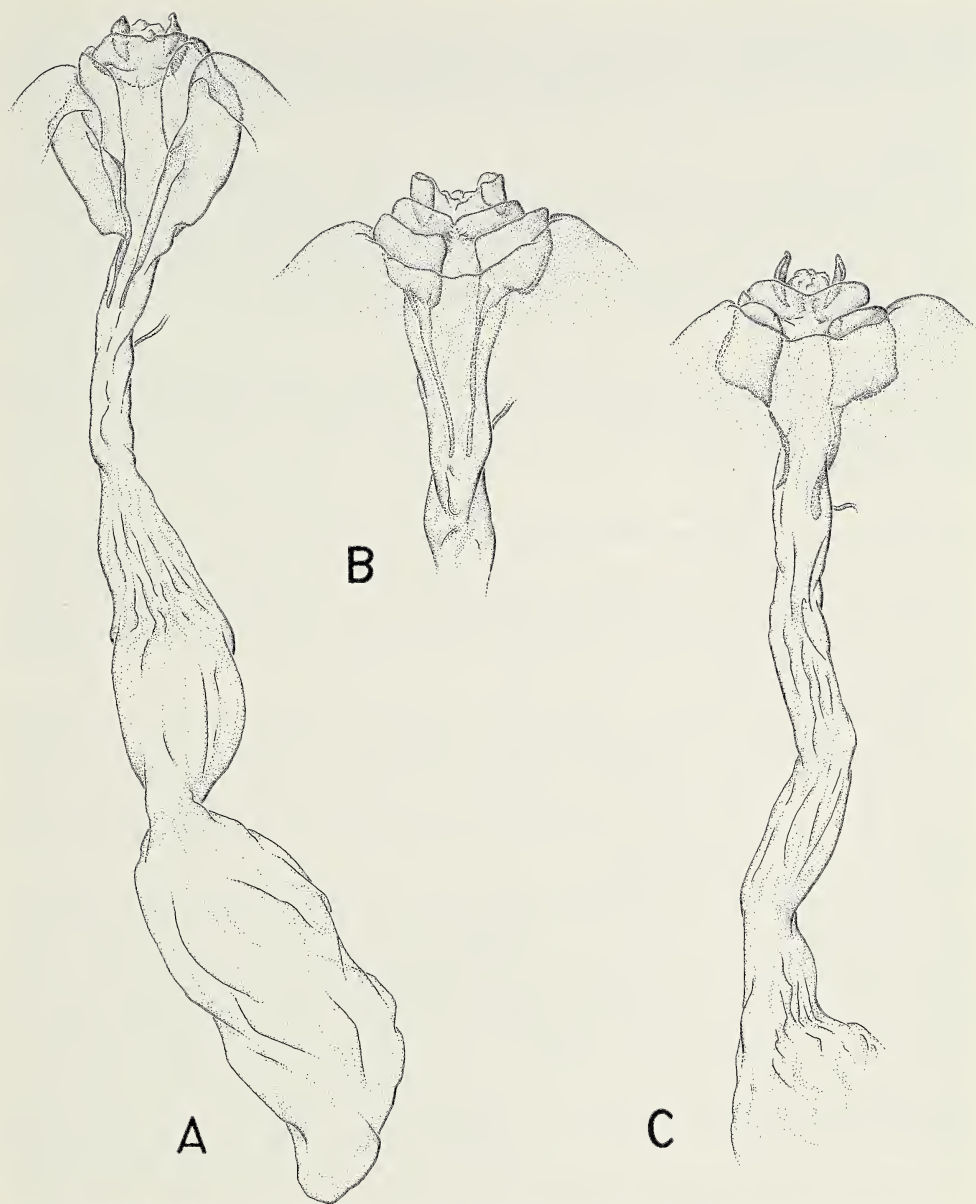


Fig. 16.—HESPERIIDAE. Female genitalia of selected species of *Panoquina*, ventral view. A. *P. ocola ocola*, Rio Baiquate bridge, SE Jarabacoa, La Vega Province, Dominican Republic, 24 July 1987, leg. Johnson and Matusik (AMNH). B. *P. hecebolus* of Fig. 14. F. Allotype, *P. ocola distipuncta*.

121 transferred to AME); NMNH—(one male, one female), data as on primary types (AMNH/HS #48, 122).

P. hecebolus in Hispaniola (new Antillean record): female, Port-au-Prince, 1–6 February 1922 (AMNH) (Fig. 14E, F), confirmed by lack of microtrichia on lamella postvaginalis (Fig. 16B); three associated males, same data (genitalia Fig. 15C), confirmed by comparison to congeners by us and S. Steinhauser. Males

must be studied further regarding their distinction from mainland *P. hecebolus*. Like other *Panoquina*, *P. hecebolus* is often associated with domestic monocots. It is possible that the Port-au-Prince occurrence is a transplantation, or that additional *P. hecebolus* have been collected from Hispaniola but not properly identified.

Remarks.—Behavior of *P. o. distipuncta*: All Hispaniolan *Panoquina* are quick flyers and hard to net, particularly if they alight only briefly on flat ground. In the upland pine forest *P. o. distipuncta* appears quickly and alights briefly for nectaring. Most specimens have been taken while nectaring on blackberry blossoms or other flowers characterizing interspersed grasslands of the upland pine habitat.

Taxonomic status of *P. o. distipuncta*: *Panoquina* has not been subject to revisionary study. We have examined and dissected many *Panoquina* taxa and specimens (see Material Examined). Concerning characters traditionally considered diagnostic of *P. ocola*, *P. sylvicola* and *P. hecebolus*, the following summary is diagnostically relevant.

We have measured the frequency of the forewing discal spot. Klots (1951), MacNeill (1975) and Riley (1975) did not mention this spot in *P. ocola*, but Scott (1986) noted its variable occurrence as a "pinpoint" in occasional specimens of *P. ocola*. Its occurrence as a mark of significant size or frequency has been considered diagnostic of *P. sylvicola* (Fig. 14B) and *P. hecebolus* (Fig. 14E). Evaluation of the occurrence of this spot in *Panoquina* identified as *P. ocola* at the AMNH indicates the following.

Of 384 specimens from 16 nations (including ten states of United States and nine states of Mexico): (i) frequency of at least pinpoint size occurrence [format: n/n = pinpoint or larger occurrence/absent]: 4/19 (Hispaniola), 2/13 (Puerto Rico), 2/19 (Brazil), 2/14 (Paraguay), 2/4 (Guatemala), 2/16 (Texas); (ii) 12 nations or states with spot absent on all specimens; (iii) eight nations or states with spot occurring in only one specimen.

We have dissected all specimens in the above-listed instances where high frequency of the discal spot occurred. In Hispaniola (4/19), all four spotted specimens were misidentified *P. hecebolus* (new Antillean record, see below). In Puebla State, Mexico (2/3) the two spotted specimens were misidentified *P. hecebolus*. In Oaxaca State, Mexico (3/3), of the three spotted specimens, two were misidentified *P. hecebolus* and one a probably undescribed species. In Nayarit State, Mexico (1/1), the spotted specimen was probably an undescribed species (not the same as that listed above under Oaxaca). In Hidalgo State, Mexico (1/1), the spotted specimen was probably also an undescribed species (not the same as either listed above under Oaxaca or Nayarit). Of 40 specimens from nine nations identified as *P. hecebolus* at the AMNH, all were dissected and determined to be *P. hecebolus*.

We conclude that, except for *P. o. distipuncta*, lack of the forewing discal spot is diagnostic of *P. ocola*. Since additional taxa appear to be present in the *Panoquina* species complex now including *P. sylvicola*, *P. ocola* and *P. hecebolus*, future studies may revise the status of *P. o. distipuncta*.

Review: In addition to the general reviews acknowledged, S. Steinhauser and A. Schwartz examined representative specimens and genitalia of *P. o. distipuncta* and other *Panoquina* as asterisked in Material Examined. S. Steinhauser also prepared additional AME material for examination; John A. Shuey and Lee D. Miller examined the materials for Fig. 15 and 16.

Etymology.—The Latinized name refers to the distinctive spot in the discal cell of the forewing.

Material examined.—We compared the type series of *P. o. distipuncta* with many *Panoquina* specimens from Hispaniola and elsewhere. Because this study constitutes the first major diagnostic study of *Panoquina* species over much of their Neotropical range, the specimens examined are listed below fully along with notes concerning their examination by specialists.

HISPANIOLA: (dissections all AMNH/HS #—; also examined by Schwartz and Steinhauser*; examined only by Steinhauser**).

1987 collections by Johnson and Matusik of *P. nero*, *P. sylvicola*, and *S. ocola* from Jarabacoa, vicinity of Jarabacoa and Bamboo Hole Canyon, La Vega Province, Dominican Republic, all circa 1000 m in the Central Cordillera: dissections AMNH, male #1*, 9*, female #13 [*P. nero*]; male #11*, 15, female #2, 16 [*P. sylvicola*]; male #14, 17, 19, 30, 31, female #12*, 18, 32, 33, 34* [*P. ocola*].

Grassland in pine forest collections by Johnson and Matusik of *P. sylvicola* in vicinities near Aceitillar, 1985, 1986, and 1987 (foothills, circa 4000 ft, Sierra de Baoruco, Pedernales Province, Dominican Republic: dissections AMNH [all *P. sylvicola*], male #10*, 35, 36, 37, 38, female #3*, 4*, 6*, 7*, 8*).

Grassland in pine forest collections of Albert Schwartz of *P. sylvicola*: 5 km NE Los Arroyos, Pedernales Province, Dominican Republic, 5300 ft, 2 July 1983 (dissections, male #20*, 21*); .6 km SE Los Arroyos, 3 July 1983 (dissections, male #22*, 23*, female #24*); Los Arroyos, 3200 ft, 11 June 1986 (dissection female #27*); 3 km SE Los Arroyos, 3200 ft, 11 June 1986 (dissection male #29*); Aceitillar, 4200 ft, August 2, 1980 (dissection male #25*), 31 July 1980 (dissection female #26*), 2 June 1987 (dissection female #28*).

Other AMNH Hispaniolan material: *P. ocola*, Sanchez, Dominican Republic, 17–21 May 1915 (dissection male #123); Bizeton, Haiti, 7 January 1922 (dissection male #124); *P. sylvicola*, Diquini, Haiti, 10 January 1922, 100 m (dissection male #125).

AME dissections of S. Steinhauser: *P. ocola*, vic. Jarabacoa, Dominican Republic, leg. J. and L. Miller, July 1987 (male, female**) by complete dissection; supportive series, same data, from undetached extruded genitalia; *P. sylvicola*, same data (male, female**) and supportive series as above.

OTHER LOCALITIES: (also examined by Schwartz and Steinhauser*; examined only by Steinhauser**), *P. sylvicola*: males—Holguin, Cuba, September AMNH Slide #G1236*; Cuba, #G1046*; Santurce, Puerto Rico, I-8-14, #G1235*; females—Ensenada, Puerto Rico; Holguin, Cuba; St. Ann's, Jamaica (AMNH/HS #53, 54, 55); AME, Colombia**, *P. ocola*: males—Canal Zone, Panama, G1047*; Colombia, #G1050*; Trinidad, #G1051*; Florida, #G1043*; Alabama, #G1048*; Brazil, #G1046*; females—Ensenada, Puerto Rico; Holguin, Cuba; St. Ann's, Jamaica (AMNH/HS #56, 57, 58); AME, Mexico**, Colombia**. *P. hecebolus*: males—Guatemala, #G1042*; Pharr, Texas, H. A. Freeman #886; Catemaco, Vera Cruz, Mexico; Valles, San Luis Potosi, Mexico; Tierra Colorado, Mexico; Candelaria, Oaxaca; Rabinal, Guatemala; Akuriman, Venezuela (AMNH/HS #126, 127, 128, 129, 130, 131); AME, Mexico**, females—Barro Colorado, Panama Canal Zone; Guatemala; Akuriman, Venezuela; Trinidad (AMNH/HS #59, 132, 133, 134); AME, Mexico**, *P. evansi* Freeman: males—Valles, Mexico, H. A. Freeman #887; Sao Paulo, Brazil, #G1729; Costa Rica, H. A. Freeman #1093*; female—Catemaco, Vera Cruz, Mexico (AMNH/HS #97). *P. viola* Evans: male—Brazil, #G1759*; female—Villaracia, Paraguay (AMNH/HS #98). *P. pauper* (Mabille): male—Belize, #G1092*; female—Santa Cruz, Bolivia (AMNH/HS #99). *P. panoquinoides* Skinner: male—Belize, #G1086*; female—Everglades, Florida (AMNH/HS #100). *P. fusina* (Hewitson): males—Amazonas, #G1726*; Obidos, Brazil, #G1712*; Peru, #G1091*; Trinidad, #G1087*; French Guiana, #G1088*; Bolivia, #G1090*, #G1089*; female—Obidos, Brazil (AMNH/HS #101). *P. bola* Bell: males—Mt. Roraima, Brazil, #G1711*; Bolivia #G1710*, #G1709*, #G1085*; female—not available. *P. luctuosa*: male—Ecuador, #G1084*; female—not available; *P. nero belli* Watson, paratype male, Ensenada, Puerto Rico (AMNH/HS #102), paratype female, same data (AMNH/HS #103).

CONSERVATION

The mesic broadleaf forests of Las Abejas are currently threatened by habitat destruction. In 1984, Matusik first noted significant deforestation from slashing and burning by Haitian and Dominican squatters converting the moist wooded areas for planting of beans and bananas. CMNH field workers at Las Abejas noted nighttime temperatures dropped steeply and that the area was covered by heavy dew (J. E. Rawlins, personal communication). This moisture probably maintains the broadleaf forest. Except for a few hours after heavy rain, we have never observed surface water in the region. Because of the lack of water, there are few, if any, permanent residents in the forests; migrant planters seed crops and return for random harvests. Near lower Abejas, approximately five acres of canopy has

been destroyed and the land planted over. Farther down the drainage much larger areas have been cleared. On two separate days in 1986 and 1987 lower and middle Abejas were filled with smoke from burning in adjacent drainages.

Administrative personnel of Ideal Dominicana, S. A. ("Ideal") maintain regular records of habitat destruction in the Parque Nacional Sierra Bahoruco [sic]. Except for locals, the area is so remote it is seldom visited. It appears that no one from the Departamento Nacional de Parques has ever been to Las Abejas. In 1987, after "Ideal" forwarded photographs of habitat destruction to park officials, we guided an army patrol into the area and it was temporarily cleared of squatters. As one method of protection, "Ideal" plans to allow the deterioration of all access roads which approach Las Abejas from Aceitillar. However, it appears doubtful there can be a permanent solution. Hopefully, the publication of these results concerning new species of butterflies at Las Abejas will offer further impetus for the protection of the Parque Nacional Sierra Bahoruco.

ACKNOWLEDGMENTS

We are particularly grateful to Albert Schwartz (MCC) who reviewed numerous drafts of this publication and examined and exchanged extensive material involving these descriptions. We are equally grateful to Stephen R. Steinhauser and Jacqueline Y. Miller (AME) who examined numerous specimens and dissections as well as provided review comments. In addition, we thank several specialists and general reviewers who reviewed various drafts of this manuscript. These include John A. Shuey (OSU) [Hesperiidae, ms. through 1986], Lee D. Miller (AME) [Hesperiidae and general review]; John E. Rawlins (CMNH), Frederick H. Rindge and Eric L. Quinter (AMNH) [general review]. Special thanks are due H. A. Freeman (Garland, Texas) for previous review comments on certain Hesperiidae, and John M. Burns (NMNH) for sharing with us results of his recently published work concerning *Hesperia nabokovi* (Hesperiidae) (Burns, 1987). This spared us having to deal with the confusing characters of certain xeric skippers whose proper generic assignment was uncertain.

Heretofore cited personnel of Ideal Dominicana, S.A., along with staff of the Museo Nacional de Historia Natural, Santo Domingo (A. Jimenez Lambertus, Director; R. Sosa, Head of Entomology; K. Guerrero, Assistant) and the Direccion Nacional de Parques gave indispensable assistance. The Carnegie expedition of 1987 was funded by the O'Neil Fund for Invertebrate Zoology; J. E. Rawlins and R. Davidson (CMNH) organized the expedition and also joined us in the field. Joe Brexa (Chicago, Illinois) accompanied the junior author in the field in 1981. Luis Marion Heredia (Santo Domingo), Robert Postelnik (Skokie, Illinois) and David Schmidt, Judith Kunreuther and Betty Manuppelli (New York, New York) provided necessary professional assistance facilitating this work.

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CORRECTION: KARYOTYPE OF *CAULOPHYLLUM THALICTROIDES*

FREDERICK H. UTECH

Associate Curator, Section of Botany

The sterile vouchers (Utech 79-081, CM 263594; two sheets) supporting the karyotype published as that of *Caulophyllum thalictroides* (L.) Michx. in the "Chromosome atlas of the vascular plants of western Pennsylvania. I" (Utech, 1980) have been reidentified as *Actaea* by Dr. William Wayt Thomas (New York Botanical Garden). The author has subsequently revisited the site and has seen numerous flowering individuals of *A. pachypoda* Ell. which has been independently verified by Dr. Robert W. Kiger (Hunt Institute for Botanical Documentation). I thank Dr. Thomas for bringing this error to my attention.

The western Pennsylvania distribution map presented for *Caulophyllum thalictroides* (Fig. 16; Utech, 1980) is correct, except for the starred voucher location. *Actaea pachypoda* is also frequent and widely distributed in rich woodlands of western Pennsylvania (Jennings, 1953; Wherry et al., 1979). The karyotypic data presented as for *Caulophyllum thalictroides* (Fig. 17, 18; Table 7; Utech, 1980) actually apply to *Actaea pachypoda*, and are in general agreement with those presented by Kurita (1959), Kawano et al. (1966) and Blair (1975) for *A. pachypoda*. *Actaea pachypoda* has two pairs of mid-sized submetacentric chromosomes, not one as in *Caulophyllum thalictroides*, although both species have the same base number of $2n = 16$.

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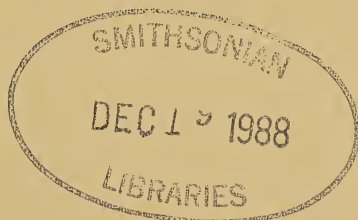
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A NEW SPECIES OF FOSSIL *BUSYCON* (*BUSYCOTYPUS*)
FROM THE LOWER PLIOCENE BUCKINGHAM FORMATION
OF FLORIDA (GASTROPODA: MELONGENIDAE)

JAY J. TRIPP

Research Associate, Section of Invertebrate Zoology

ABSTRACT

A new species of the melongenid genus *Busycon* (*Busycotypus*), characterized by the double coronation of its carinae, is described from the early Pliocene Buckingham Formation of the Newburn Mine, Sarasota, Sarasota County, Florida. This taxon, *Busycon* (*Busycotypus*) *bicoronatum*, new species, appears synchronic with *B. (B.) pyrum floridanum* Olsson & Harbison, but distinct from it.

INTRODUCTION

In September 1983, two specimens of unique form were found at the highly fossiliferous Newburn Mine—at that time known as the Macasphalt Company (Division of Ashland Oil, Inc.), No. 0800826—Newburn Road, Sarasota, Sarasota County, Florida. These specimens were taken from a spoil bank created by operating drag-lines in this working mine, and therefore could not be assigned to one particular stratigraphic unit. However, the species is obviously from the Lower Pliocene Buckingham Formation (formerly called Pinecrest Beds; Petuch, 1986, 1987) which comprises most of the exposed profile of the Newburn Mine. These two specimens from 1983 were retrieved along with numerous examples of other Pliocene species, such as well-preserved *Hystrivasum locklini* (Olsson & Harbison), very large *Arcinella cornuta* (Conrad), *Turbinella regina* Heilprin, *Contraconus adversarius* (Conrad), *Siphocypraea carolinensis floridana* (Mansfield), and *Pyruella rugosicostata* Petuch.

Subsequent collecting at this site by the author has produced, rather infrequently, additional examples of this new species. An example from the type locality was collected in 1978 by Ms. Mary Palmer of Alva, Florida, and loaned to become a part of the type lot. These remarkable specimens belong to an undescribed species of the subgenus *Busycotypus*, here named *Busycon* (*Busycotypus*) *bicoronatum*, new species, (Fig. 1, 2, 5-7, 9, 12).

SYSTEMATICS

Busycon (*Busycotypus*) *bicoronatum* Tripp, new species

Fig. 1-12

Holotype.—(Incomplete; nuclear whorl and outer lip margin are damaged): height 95 mm; width 45 mm; spire 23 mm from apex to end of sutural line; body whorl 85 mm including siphonal canal; siphonal canal 45 mm from end of columella, with average width of 6 mm; aperture 32 × 21 mm not including siphon; width of shoulder at sutural end 10 mm; width of channel at sutural end 9 mm; number of whorls 7; spiral cords at end of shoulder 3; width of shoulder at sutural

Submitted 28 January 1988.

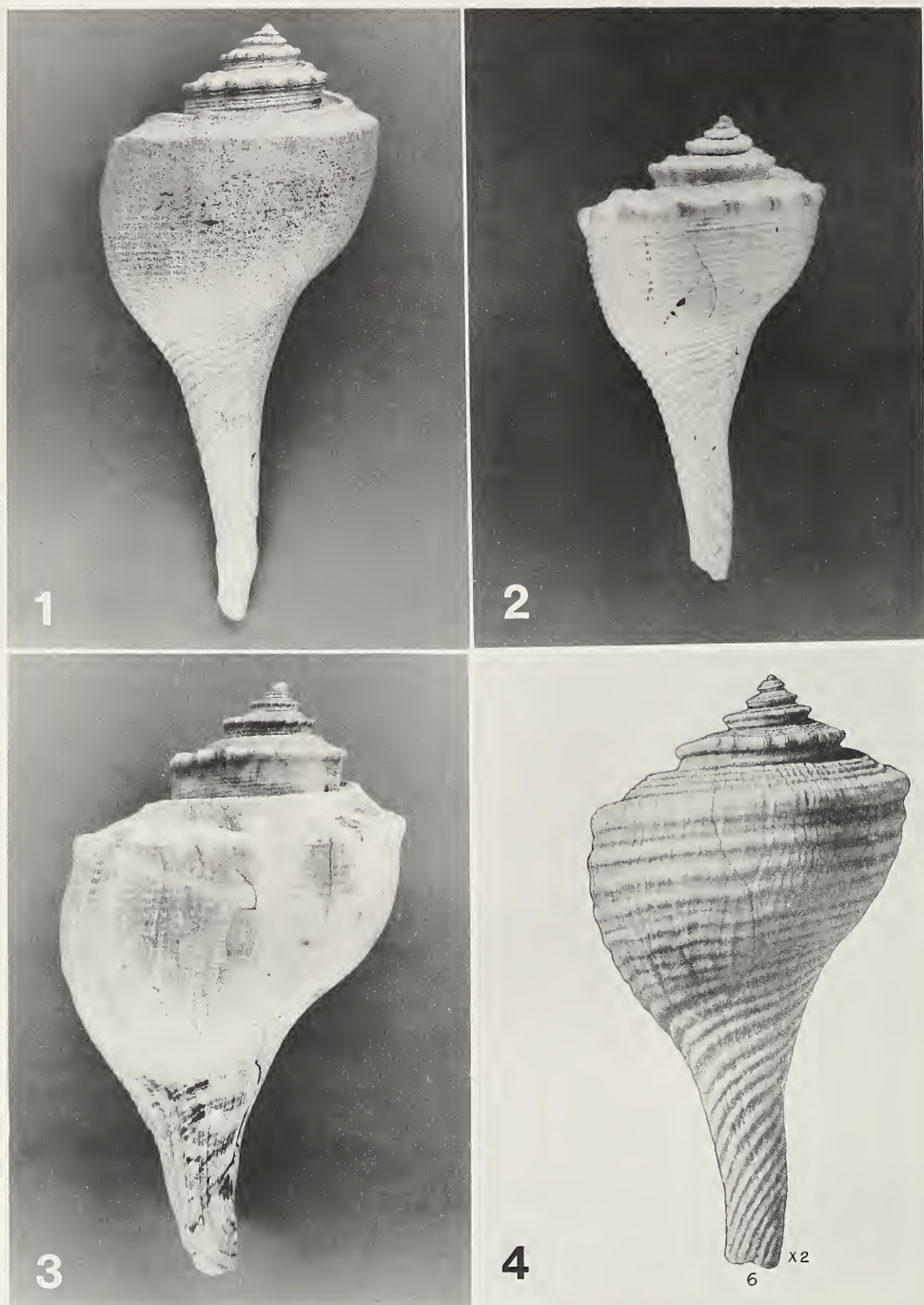


Fig. 1-4.—Dorsal views of *Busycon* species. 1. *Busycon* (*Busycotypus*) *bicoronatum*; Holotype, CM No. 47197. Height, 95 mm. 2. *B. (B.) bicoronatum*; Paratype 1, CM No. 47198. Height, 45 mm. 3. Recent *B. (Busycotypus) canaliculatum* (Linnaeus), juvenile. Height, 91 mm. 4. *B. pyrum aepynotum* (Dall); type, United States National Museum No. 112026, Alum Bluff, upper bed, Apalachicola River, western Florida, Lower Pliocene (after Mansfield, 1930).

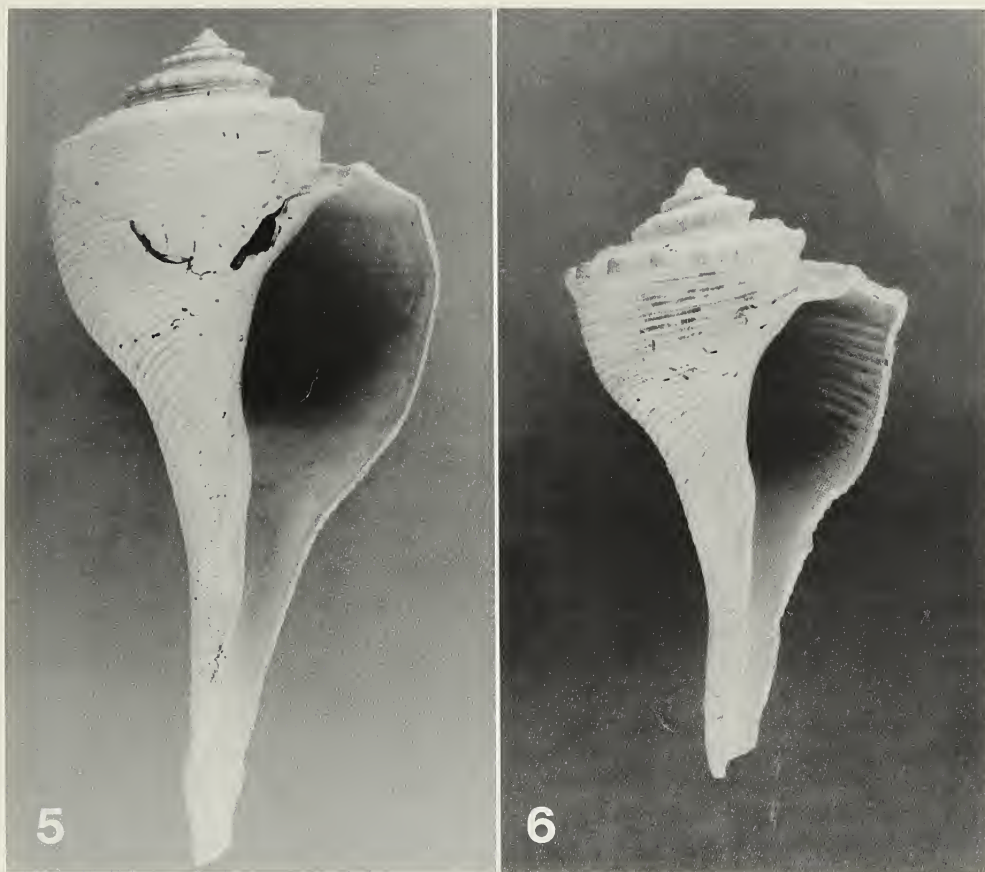


Fig. 5, 6.—Ventral view of *Busycon* (*Busycotypus*) *bicoronatum*. 5. Holotype, CM No. 47197. Height, 95 mm. 6. Paratype 1, CM No. 47198. Height, 45 mm.

end 10 mm; width of channel at sutural end 9 mm; width of channel at second whorl 2 mm; three spiral threads between last suture and carination.

Type locality.—A spoil bank, Newburn Mine, Apac Fla., Inc. (Ashland Oil, Inc.), D. O. T. 17-087, Newburn Road, roughly five miles east of Sarasota, Sarasota County, Florida, 11 September 1983, Carnegie Museum (= CM) No. 47197 (Fig. 1, 5, 7).

Paratype 1.—Juvenile, height 45 mm, width 25 mm, spire 16.5 mm, body whorl 40 mm, siphonal canal 22 mm, aperture 19×9.5 mm; same locality and date as holotype, CM No. 47198 (Fig. 2, 6, 9, 12).

Paratype 2.—Height 55 mm, width 25 mm, collected 1978, Warren Bros. Pit (= Apac Fla., Inc.), Sarasota, Sarasota County, Florida, in the collection of Ms. Mary Palmer, Alva, Florida.

The following seven paratypes are in the collection of the author, from the same locality as the holotype:

Paratype 3.—(No. 2.221-j of the lot): Height 61 mm, width 26 mm, collected 30 November 1986, CM No. 47201.

Paratype 4.—(No. 2.221-i of the lot): Height 39 mm, width 28 mm, collected 25 October 1986, CM No. 47202.



Fig. 7, 8.—Apical views of *Busycon* (*Busycotypus*) species. 7. *B. (B.) bicoronatum*; holotype. Width, 45 mm, CM No. 47197. 8. Recent *B. (B.) canaliculatum* (Linnaeus), juvenile, same specimen as Fig. 3. Width, 55 mm.

Paratype 5.—(No. 2.221-e of the lot): Height 45 mm, width 18 mm, collected 16 August 1986, CM No. 47203.

Paratype 6.—(No. 2.221-a of the lot): Height 31 mm, width 17 mm, collected 10 October 1985, CM No. 47204.

Paratype 7.—(No. 2.221-f of the lot): Height (tip of canal missing) 45 mm, width 25 mm, collected 20 September 1986, CM No. 47205.

Paratype 8.—(No. 2.221-d of the lot, with badly broken lip): Height 29 mm, width 15 mm, collected 19 May 1986, CM No. 47206.

Paratype 9.—(No. 2.221-h of the lot): Height (tip of canal missing) 51 mm, width 31 mm, collected 11 October 1986, CM No. 47207.

Additional Material Examined.—Eight additional incomplete specimens were collected with the help of Mr. Thomas Ketter at the type locality in 1986, the largest of which measures 108 mm in height. Although mostly complete early whorls and/or upper body whorls only, these fragments are recognized as belonging to *Busycon* (*Busycotypus*) *bicoronatum*, new species.

Description.—The adult holotype is dextrally coiled, pyriform, slender, and lightweight. The protoconch, partially broken, comprises the first one and one-half apical whorls. The spire, protracted and scalariform, with seven whorls, forms an angle of 65°. The height of the spire is less than one-fourth of the total height of the shell. Each whorl has a double carina with fine, close, and regular crenulations on each. On the body whorl, which is $\frac{9}{10}$ of the height of the shell, the crenulations of the outer carina form 18 knobs on the middle section of the spire, but smooth out to become almost a rounded rib near the aperture. The suture forms a very wide, deep, channeled sulcus. This sulcus, 9 mm wide on the penultimate whorl, slopes inward toward the suture, and is smooth except for very

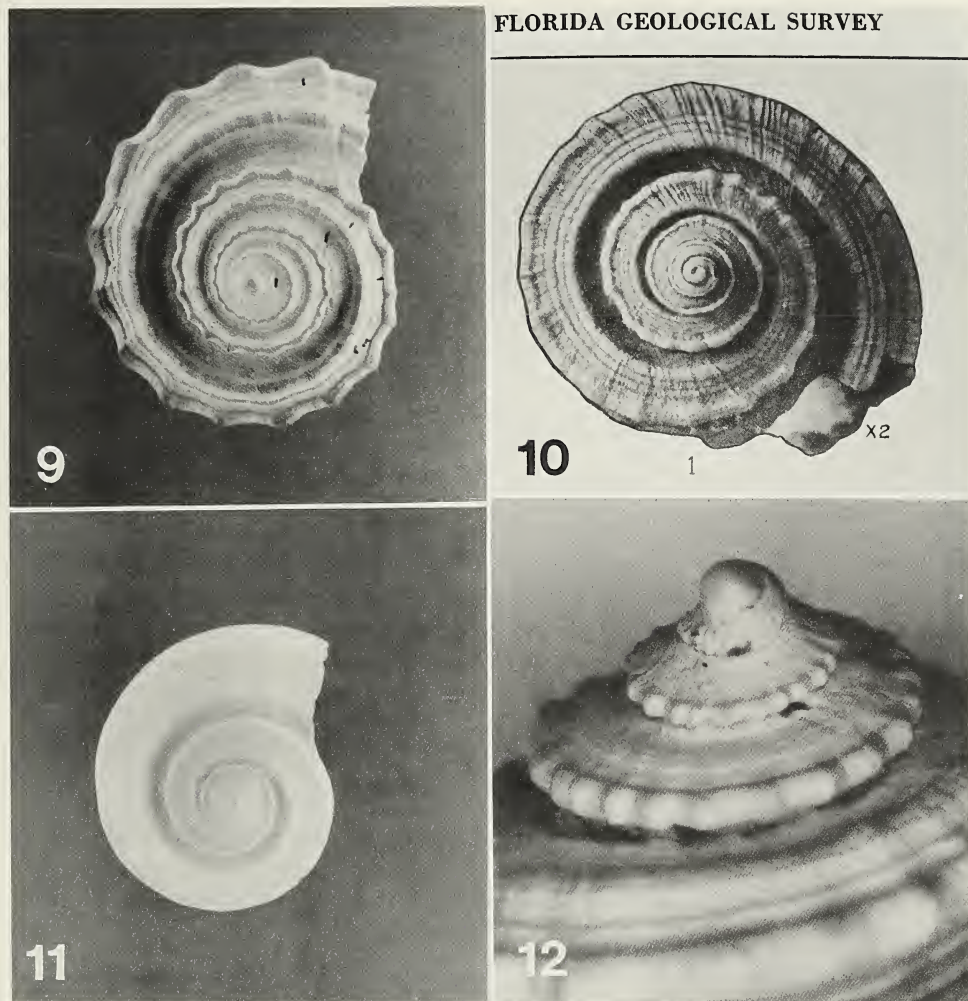


Fig. 9–12.—Apical details of *Busycon* species. 9. *B. (Busycotypus) bicoronatum*; Paratype 1, CM No. 47198. Width, 25 mm. 10. *B. pyrum aepynotum* (Dall); United States National Museum No. 112026, Alum Bluff, upper bed, Apalachicola River, western Florida, Lower Pliocene (after Mansfield, 1930). 11. *B. pyrum floridanum* Olsson & Harbison; Buckingham Formation, Sarasota, Florida. Width, 27 mm. 12. Protoconch of *B. (B.) bicoronatum*; Paratype 1, CM No. 47198.

fine, close oblique wrinkles of growth. The shoulder is slightly concave, with three spiral cords at the end, crossed by irregular, sometimes waving, lines of growth. The aperture is oval-elongate, corresponding in height to one-third of the total height of the shell, with its upper end elevated, forming a narrow sinus. Its marginal lip is broken, but inside, at the top near the shoulder, faint lirae remain. The deep interior is smooth and shiny. The surface of the shell is sculptured with evenly-spaced, prominent but fine, spiral ridges, including the area between the carinae. The columella has a faint glaze remaining, with one rather long, oblique ridge or plait crossing the pillar at the point where the siphonal canal bends slightly; the spiral ridges also show lightly across the top of the columella.

Paratype 1, CM No. 47198: this is a juvenile, also dextral, with a nucleus of one and one-half smooth, globose whorls; typical sculpture begins on the second half of the first post-nuclear whorl; four post-nuclear whorls are present; body whorl is strongly-knobbed. Spire angle is 61° , more acute than that of the holotype, and almost tilted or depressed on the dorsal side. Interior of outer lip has close, strong lirae, and a smooth, deep interior. Space between the two carinae bears only two horizontal ridges; finer secondary cords are mid-way between major spiral cords on the body whorl. All other features correspond to the adult, as in the holotype.

Etymology.—This new species is named for the doubly carinate whorls which adorn the spire.

Remarks.—This distinctive busyconine species is rare at the type locality, and has seemingly been collected only when the mine is digging into the lower level. The material described in this paper was found only in the central part of the pit, as it now exists. In all probability, the species developed and died out within a relatively short interval of the Lower Pliocene, because weekly collecting by the author during the first three months of 1987 has been devoid of any additional specimens of this species. At the current time, index fossils of the younger Caloosahatchee Formation are commonly found, such as *Hystrivasum horridum* (Heilprin), a small number of *Siphocypraea problematica* (Heilprin), *Chicoreus* (*Chicoreus*) *floridanus* Vokes, and *Murex* (*Phyllonotus*) *pomum* Gmelin, among others.

Busycon (*Busycotypus*) *bicoronatum* is apparently a taxon from the lineage of species characterized by the living and well-known *Busycon* (*Busycotypus*) *canaliculatum* (Linnaeus) (Fig. 3, 8), from which it differs (comparing specimens of similar size) by its more slender form, longer siphonal canal, deeper and wider sutural channel, less scalariform spire, stronger surface ridges, and strongly-knobbed sutural margins, as opposed to the beaded sutures in *Busycon* (*Busycotypus*) *canaliculatum*.

Comparisons.—*Busycon* (*Sycotypus*) *concinnum* Conrad (1875) from King's marl pit, Sampson County, North Carolina, is similar in some features to the new species. Both have strongly carinated and scalariform early whorls, with definite, but fine, horizontal ridges over the entire surface. However, on *B. concinnum* the body whorl lacks low knobs and retains only a suggestion of the carina on the lift of the posterior apertural lip. *Busycon concinnum* has only a single carina on the whorls; in addition, the body whorl declines more rapidly to the canal. *Busycon* (*Busycotypus*) *bicoronatum* is more graceful, with a longer canal, narrower body whorl, and very narrow aperture.

Busycon (*Busycotypus*) *pyrum floridanum* Olsson & Harbison, 1953 (Fig. 11), has a wide, deep sulcus and a double carina after the suture. The outer of the two ridges bears tiny raised beads on the spire whorls only. On the mature body whorl, this coronation becomes obsolete, the carina becoming a smooth cord. The coronation is never as intense as in the new species. In *Busycon* (*Busycotypus*) *bicoronatum*, the coronation of the carinae carries into the adult stage, and the spire is much more scalariform. *Busycon pyrum floridanum* has a profile with a less pronounced spire overall. Known specimens of the new species are smaller than the larger specimens of *B. pyrum floridanum*.

Busycon excavatum (Conrad, 1840), from the Upper Miocene, has the deep, wide sutural sulcus of *B. bicoronatum*, but it lacks the very strong coronation of the new species.

Fulgur pyrum var. *aepynotum* Dall, 1890 [holotype: United States National Museum No. 112026, from the Lower Pliocene of Alum Bluff (upper bed, Apalachicola River, western Florida)], is quite similar to the new species. Dall did not figure his variety, but gave only the brief description, "has a medium sutural canal, an excavated keeled shoulder, undulate or subtuberculate and very coarse, broad spirals with wider interspaces." Dall stated that the largest specimen he had seen was 30 × 50 mm. The largest, but easily recognizable, fragment in the type material of the new species measures 108 mm, and still retains the constant features of the species, although the body whorl is largely missing.

Mansfield (1930, pl. 8, figs. 1, 6) later figured Dall's specimen as *Busycon pyrum aepynotum* (Dall, 1890), apically and dorsally only (reproduced here in Fig. 10 and Fig. 4, respectively), and believed it to be closely related to *Busycon pyrum incile* from the Yorktown Formation of Virginia. Gardner (1944) reillustrated Mansfield's figure of Dall's *B. p. aepynotum* (pl. 50, fig. 12).

The dorsal view of Mansfield's figure of *B. p. aepynotum* shows a stout, solid shell, less graceful than *B. bicoronatum*, and proportionately shorter, the width equalling one-half the height (Fig. 4). In *B. bicoronatum* the width is less than half the height. The outside cord at the shoulder of *B. p. aepynotum*, although certainly a juvenile at 43 mm, is very strong, but does not have the heavy tubercles of the *B. bicoronatum* crown. The holotype of *B. aepynotum* appears to carry one true corona on the apical whorls to the outside of the shoulder. In contrast, all specimens of comparable size in the type lot of *B. bicoronatum* have distinctly doubled carinae.

Spiral cords on the body whorl of *B. p. aepynotum* are fewer, stronger, more pronounced, and more rugged than those of *B. bicoronatum*. On the other hand, the body cords of *B. bicoronatum* are more numerous and much finer, and tend to become obsolete near the bottom of the canal as they descend. The heavy, coarse spirals of *B. p. aepynotum* continue in strength to the very tip of the canal. The major spiral cords on the body whorl of the new species tend to have finer minor cords between them. These secondary cords are not apparent on Mansfield's figure of *B. p. aepynotum*. These dissimilarities between *B. bicoronatum* and *B. p. aepynotum* are constant throughout the known material of *B. bicoronatum*, where the deviation of characters is very slight.

In view of these marked differences between *B. aepynotum* and *B. bicoronatum*, the new material warrants species recognition. The Recent busyonines have a limited distribution due to the lack of an active free-swimming larval stage, caused by the loss of the velum before the animal emerges from the egg-capsule (Puffer and Emerson, 1954). *B. aepynotum* is distinct, although perhaps synchronic, with the Lower Pliocene taxon found farther south, here named *B. (Busycotypus) bicoronatum*.

In summary, the presumably derived features that distinguish the new species from all others are the scalariform spire, the wide, deep sutural channel, and the highly-coronated double carina, with prominent but fine major and minor cords evenly spaced on the body whorl.

Considering the similarity of general characteristics within this particular group of sulcate species from the Upper Miocene or Lower Pliocene to Recent, which prevails in the extant species *Busycon (Busycotypus) canaliculatum* (Linnaeus), it is hypothesized that the group conforms to the biological concept of a superspecies, an evolutionary assemblage of closely related species distinguished by slight, but consistent morphological differences. If the morphological criteria for separating

other species of *Busyconinae*, living or formerly coeval, are accepted, then *Busycon* (*Busycotypus*) *bicoronatum* constitutes another suitably characterized species in the subfamily.

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MIDDLE PLEISTOCENE ARVICOLINE RODENTS AND
ENVIRONMENTAL CHANGE AT 2900-METERS ELEVATION,
PORCUPINE CAVE, SOUTH PARK, COLORADO

ANTHONY D. BARNOSKY

Assistant Curator, Section of Vertebrate Fossils

DONALD L. RASMUSSEN¹

Research Associate, Section of Vertebrate Fossils

ABSTRACT

Porcupine Cave is the highest elevation site in Colorado from which abundant Pleistocene mammal bones have been found and one of few such high-elevation sites known in the world. One of the seven fossiliferous localities in the cave, The Pit, has a stratigraphic section at least 3 m thick that apparently spans one or more glacial-interglacial cycles, a tentative interpretation based on the alternation of loess and dark brown organic-rich clay pellets. The loess at the top of The Pit contains *Pitymys meadensis*, *Microtus paroperarius*, *Ondatra* cf. *annectens*, *Mictomys* near *meltoni*, a primitive morphotype of *Lagurus curtatus*, and *Microtus montanus* or *M. longicaudus*. This sympatry extends the biochronologic range of the first four species upward, or the last two downward, or both, and suggests an age near 400 ka. At least 43 other mammal, bird, and herptile species are represented in the fauna, including some that are extinct, some that today live only at lower elevations either west or east of the site, and some that presently survive in the Porcupine Cave region.

INTRODUCTION

The Pleistocene mammal record of Colorado is not well known in comparison to that of the eastern, midwestern, and southwestern United States (see summaries in Kurtén and Anderson, 1980; Lundelius et al., 1983; Harris, 1985; Graham and Mead, 1987). Yet the diverse topography in Colorado, where elevations range from less than 1500 meters in the eastern Plains to more than 4200 meters in the high Rocky Mountains, demands fossil mammals from a correspondingly diverse range of sites to understand Pleistocene biogeographic and evolutionary patterns.

In recent years the network of Pleistocene mammal data in Colorado has been growing. At least faunal lists have been published for nine late-Wisconsinan sites from east of the continental divide, most of them from the northeastern Plains (Kurtén and Anderson, 1980; Harris, 1985). One study has been done on a late-Wisconsinan fauna from the mountainous Western Slope (Emslie, 1986).

Published literature exists for only two pre-Wisconsinan Pleistocene mammal faunas. The Mesa de Maya fauna comes from the southeast corner of Colorado at approximately 1800 m elevation (Hager, 1974). We do not consider it further here because it lacks extinct arvicolines. The Hansen Bluff site is in the San Luis Valley at about 2300 meters elevation and produced several superposed faunules and other paleoenvironmental information for the time spanning ca. 700 to 880 ka (Rogers et al., 1985).

Initial work at a third pre-Wisconsinan site—Porcupine Cave—forms the basis of this report. Although excavation of the extensive deposits still is underway,

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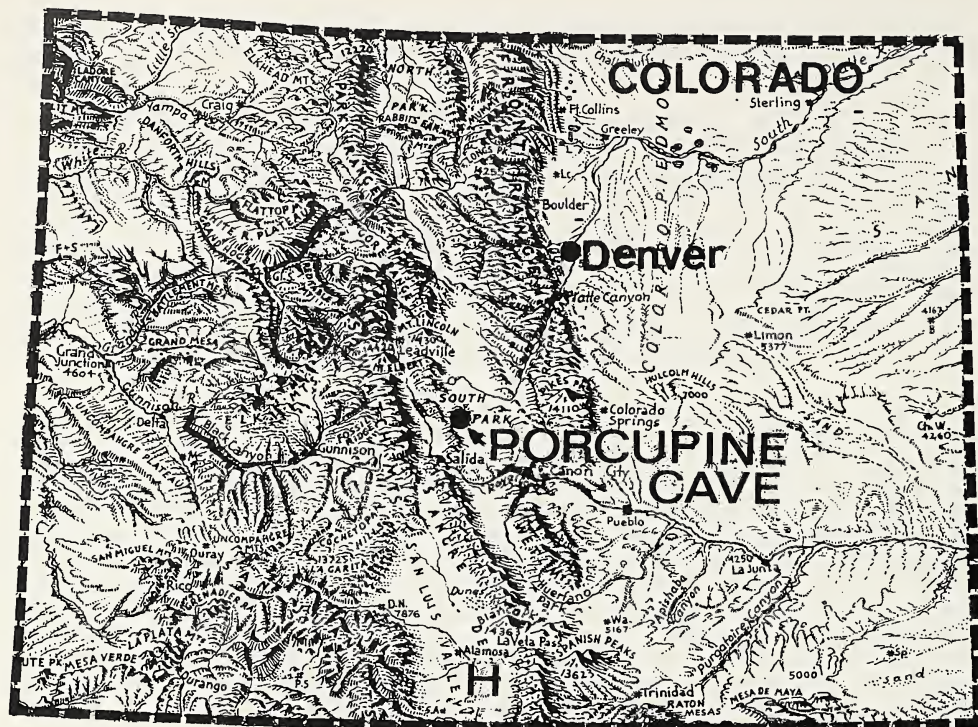


Fig. 1.—Location of Porcupine Cave and Hansen Bluff (= H). Base map is from Atwood (1940).

the information recovered thus far is of particular interest in (1) documenting the highest-elevation Pleistocene fauna known in North America; (2) establishing a biostratigraphic age of ca. 400 ka for the site; and (3) recognizing sedimentary and faunal changes that may correlate with at least one glacial-interglacial transition.

Geographic and Geologic Setting

Porcupine Cave is located in Park County, approximately 50 km south of Hartsel, Colorado (Fig. 1). Map coordinates are: NW $\frac{1}{4}$ of SW $\frac{1}{4}$ Sec. 23, T15S, R76W, Lat. $38^{\circ}43'45''$ N, Long. $105^{\circ}51'41''$ W, Gribbles Park 7.5' Quad. At 2900 m elevation, the cave lies high on the southwest rim of South Park within the early Ordovician Manitou Dolomite, which locally strikes $N10^{\circ}$ W and dips ap-

Table 1.—Common names of plants mentioned in the text.

<i>Abies</i>	fir
<i>Artemisia</i>	sagebrush
<i>Cercocarpus</i>	mountain mahogany
<i>Chrysothamnus</i>	rabbit bush
<i>Coryphantha</i>	ball and nipple cactus
<i>Elymus</i>	wild rye grass
<i>Festucca</i>	fescue grass
<i>Juniperus</i>	juniper
<i>Lithospermum</i>	puccoon
<i>Muhlenbergia</i>	mountain muhly
<i>Opuntia</i>	prickly pear cactus
<i>Oryzopsis hymenoides</i>	Indian ricegrass
<i>Pediocactus</i>	mountain ball cactus
<i>Picea</i>	spruce
<i>Pinus edulis</i>	piñon pine
<i>Pinus ponderosa</i>	ponderosa pine
<i>Pseudotsuga menziesii</i>	Douglas fir
<i>Yucca glauca</i>	Spanish bayonet or yucca

proximately 30°E. Capping the Manitou Dolomite is an orthoquartzite facies of the middle Ordovician Harding Sandstone. The Manitou and Harding form a prominent ridge, which has been topographically expressed at least since Paleogene time. The ridge apparently was buried during the Oligocene by volcanoclastics of the Thirty-Nine Mile Volcanic Field or slightly older sediments, then exhumed in the Neogene. Cave formation had probably begun by the Oligocene and proceeded in several stages through the action of water and/or sulfur-rich solutions as evidenced by water-worn passages, high domes, truncation and erosion of large speleothems, fissures and passages filled with cave breccia, and the abundance of calcareous, sulfate, and sulfide minerals. DeVoto (1971) discusses additional aspects of the geology of South Park.

The cave opens on a west-facing slope in a region sparsely vegetated predominantly with *Pinus ponderosa*, *Pinus edulis*, *Pseudotsuga menziesii*, *Juniperus*, *Artemisia*, *Chrysothamnus*, *Cercocarpus*, *Yucca*, *Coryphantha*, *Opuntia*, grasses, and several small herbaceous plants (see Tables 1 and 2 for common names of taxa). Armstrong (1972:27) places the site at the ecotone between montane grassland and coniferous forest. Küchler's (1964) more detailed vegetation map shows the ecotones between *Festucca-Muhlenbergia* grassland, *Pinus-Pseudotsuga* needleleaf forest, and *Picea-Abies* needleleaf forest near the opening of Porcupine Cave. Approximately 57 species of mammals live within 100 km of the site now or did live there in historic time (Table 2 and Armstrong, 1972).

Similar flora and fauna apparently prevailed at Porcupine Cave as far back as 2000 years ago, as documented by macrofossils from the Trail Nest, a *Neotoma cinerea* midden 100 m north of the cave entrance. A sample composed of material from 3 to 10 cm above the bottom of the 25-cm thick midden was dated at 2180 ± 80 yr BP (BETA-21029) and included predominantly needles of *Pinus ponderosa*, *Pinus edulis*, and *Pseudotsuga menziesii*, with fewer fragments of *Cercocarpus*, *Chrysothamnus*, *Pediocactus*, *Yucca*, *Opuntia*, *Lithospermum*, *Oryzopsis hymenoides*, and *Elymus*. Teeth of *Microtus* sp. and a complete specimen of the beetle *Eleodes* also are represented. All of these taxa presently occur in South Park.

Table 2.—Preliminary list of fossil mammals from Porcupine Cave. Carnivores were identified by Elaine Anderson (Denver Museum of Natural History).

Taxon	CM locality number							
	1925	1926	1927	1928	1929	1930	1931	1932
Soricidae (shrews)	X							
Chiroptera (bats)	X							
<i>Ochotona</i> cf. <i>princeps</i> (pika)	X		X					
<i>Lepus</i> spp. (hares and jackrabbits)	X	X	X	X				X
<i>Sylvilagus idahoensis</i> (pygmy rabbit)*	X		X					X
<i>Sylvilagus</i> sp. (cottontail rabbit)	X	X	X	X				X
<i>Eutamias</i> sp. (chipmunk)	X	X	X	X				X
<i>Marmota</i> sp. (marmot)	X	X	X	X				X
<i>Cynomys</i> sp. 1 (prairie dog)	X							
<i>Cynomys</i> sp. 2 (prairie dog)			X					
<i>Spermophilus</i> spp. (ground squirrels)	X	X	X	X				X
<i>Sciurus</i> sp. (tree squirrel)	X		X					X
<i>Tamiasciurus</i> (pine squirrel)	X		X					X
<i>Thomomys</i> (pocket gopher)	X		X					X
<i>Neotoma cinerea</i> (bushytail packrat)	X	X	X					X
<i>Neotoma</i> sp. (small packrat)	X	X	X					X
<i>Pitymys meadensis</i> (Meade vole)†	X	X	X					X
<i>Microtus paroperarius</i> (tundra vole)†	X							
<i>M. pennsylvanicus</i> (meadow vole)			X					
<i>M. montanus/longicaudus</i> (montane or longtailed vole)	X							
<i>Lagurus curtatus</i> (sagebrush vole)*	X	X	X					X
cf. <i>Phenacomys</i> (heather vole)	X							
<i>Mictomys</i> near <i>M. meltoni</i> (Melton's bog lemming)†	X							
<i>Ondatra</i> cf. <i>annectens</i> (Brown's muskrat)†	X							
<i>Erethizon</i> sp. (porcupine)	X		X					
<i>Canis latrans</i> (coyote)	X		X	X				X
<i>Canis lupus</i> (wolf)				X				
<i>Vulpes</i> sp. (fox)	X							
<i>Martes</i> sp. (marten)				X				
<i>Mustela</i> cf. <i>nigripes</i> (ferret)	X					X		
<i>Mustela frenata</i> (weasel)	X							X
<i>Mustela vison</i> (mink)	X							
<i>Spilogale</i> sp. (skunk)	X			X				X
<i>Taxidea taxus</i> (badger)	X			X	X			X
<i>Gulo</i> sp. (wolverine)								X
possibly <i>Acinonyx</i> (cheetah)†	?							
<i>Lynx</i> sp. (lynx or bobcat)								X
<i>Cervus canadensis</i> (wapiti elk)	X							
<i>Odocoileus</i> sp. (deer)	X							
<i>Antilocapra</i> sp. (antelope)	X							
<i>Ovis</i> cf. <i>canadensis</i> (bighorn sheep)	?							
<i>Camelops</i> sp. (camel)†	X		X					
<i>Equus</i> sp. (North American horse)†	X							

* Extant, not found within 100 km of the site in historic times.

† Extinct. ? Questionable identification.

Discovery and History of Investigation

The entrance to Porcupine Cave is through an adit that was constructed by miners in the late 1800s as they followed a mineralized vein in the dolomite for approximately 15 m. By 1920 cavers were exploring Porcupine Cave on a regular basis but it was not until some 50 years later that the first map was published

(Parris, 1973). In 1981 fossil bones were discovered by Larry Rasmussen during casual exploration, which led to reconnaissance by personnel from The Carnegie Museum of Natural History (CM) in 1985. Preliminary excavation began in 1986 and continued in 1987, resulting in the fossils that form the basis for this report and in discovery of new cave passages that increased the known size of Porcupine Cave by at least 40% (Branson and Rasmussen, 1987). Completion of the excavation, survey, and faunal analysis will require several more seasons of work.

METHODS

Fossil vertebrates reported here were collected from seven localities within the cave: The Pit (CM loc. 1925), Gypsum Room (CM loc. 1926), Velvet Room (CM loc. 1927), Badger Locality (CM loc. 1928), Damp Room (CM loc. 1929), Ferret Room (CM loc. 1930), and New Passage Room (CM loc. 1931). Material that was collected without regard to specific locality is cataloged as "Porcupine Cave Undifferentiated" (CM loc. 1932). All Porcupine Cave specimens mentioned herein, as well as detailed locality information and maps, are stored at The Carnegie Museum of Natural History, Section of Vertebrate Fossils.

The Pit and the Velvet Room each were gridded into 0.91-m (3 feet) square grids and each grid was excavated stratigraphically (Fig. 2, 3). Strata were divided into beds corresponding to prominent lithologic changes and thick homogenous beds were divided further into arbitrary excavation levels of approximately 0.3 m. Depths were measured down from a permanent datum established at or above floor level at each excavation site. Before excavation the highest part of the cave floor was 0 cm (= cm below datum) in The Pit and -17.8 cm in the Velvet Room.

Sediment from each level was passed through a graded series of sieves. For The Pit excavation the sieve meshes were 2, 4, 8, 16, 20, and 30 squares/2.54 cm (1 inch); for the Velvet Room they were 4, 8 and 20 squares/2.54 cm. Fossils were picked without aid of magnification from residues coarser than 20 mesh; the 20 and 30-mesh size-fractions have yet to be picked. Sediment from Levels 1 through 3 of The Pit and from the Velvet Room was dry-screened but soaking for 24 hours and wet-screening was necessary to disaggregate the clays in Levels 4 and 5 of The Pit and from the Gypsum Room. Fossils from other localities were collected from the surface of the cave floor down to 0.3 m below it. Sediment samples from below The Pit excavation were obtained with a 5.1 cm (2-inch) diameter, 20.3 cm long (8-inch) bucket auger.

Dental terminology for arvicoline teeth generally follows van der Meulen (1978) and Martin (1987), except in numbering of triangles and reentrants of M^3 for which a more common convention is followed (Fig. 4c, d). Repenning's (1983) terms "primary wings" and "secondary wings" are added for the anterior structures of M_1 because they are as precise as van der Meulen's notation but in certain cases are less cumbersome to read and write (but see Martin, 1987, for a contrasting opinion). The relevant synonymies between Repenning's terms and those favored by van der Meulen (1973, 1978) and Martin (1987) are: primary wings = T4 and T5, secondary wings = T6 and T7 (see also Fig. 4). "Anterior cap" as used here equates with van der Meulen's (1973:33) "AC2" for *Lagurus* and *Microtus* but "AC3" for *Pitymys*.

Measurements in Tables 3, 4, and 5, and the statistics derived from them were obtained through the R & M Biometrics BIOQUANT image-processing system, which digitizes the image of specimens as projected on a computer monitor through a video camera that looks through a Wild M8 microscope at 25 \times magnification. The rest of the measurements were taken with a reticule on a Wild M3 microscope at 16 \times for *Ondatra* teeth and 25 \times for other taxa.

All minimum distances are measured from the inner (dental) margin of the enamel band, whereas maximum distances are measured to the outer margin of the enamel band (Fig. 4, 5, and 6, 7). Measurements are diagrammed in Figures 4 and 6.

We use the term "loess" for "a homogeneous, non-stratified, unindurated deposit consisting predominantly of silt, with subordinate amounts of very fine sand and/or clay" (American Geological Institute, 1962). Rock and sediment colors are designated as the closest match to the Geological Society of America Rock Color Chart (1984).

ABBREVIATIONS

AC, anterior cap. ACC, anteroconid complex. AL, anterior loop. BETA, Beta Analytic, Inc. BRA, buccal reentrant angle. Cac, minimum distance across the most anterior constriction on the anterior cap. CM, The Carnegie Museum of Natural History. Cpw, maximum distance from the apex of buccal reentrant 2 to the posterior margin of triangle 5, measured parallel to the long axis of the tooth. Csw,

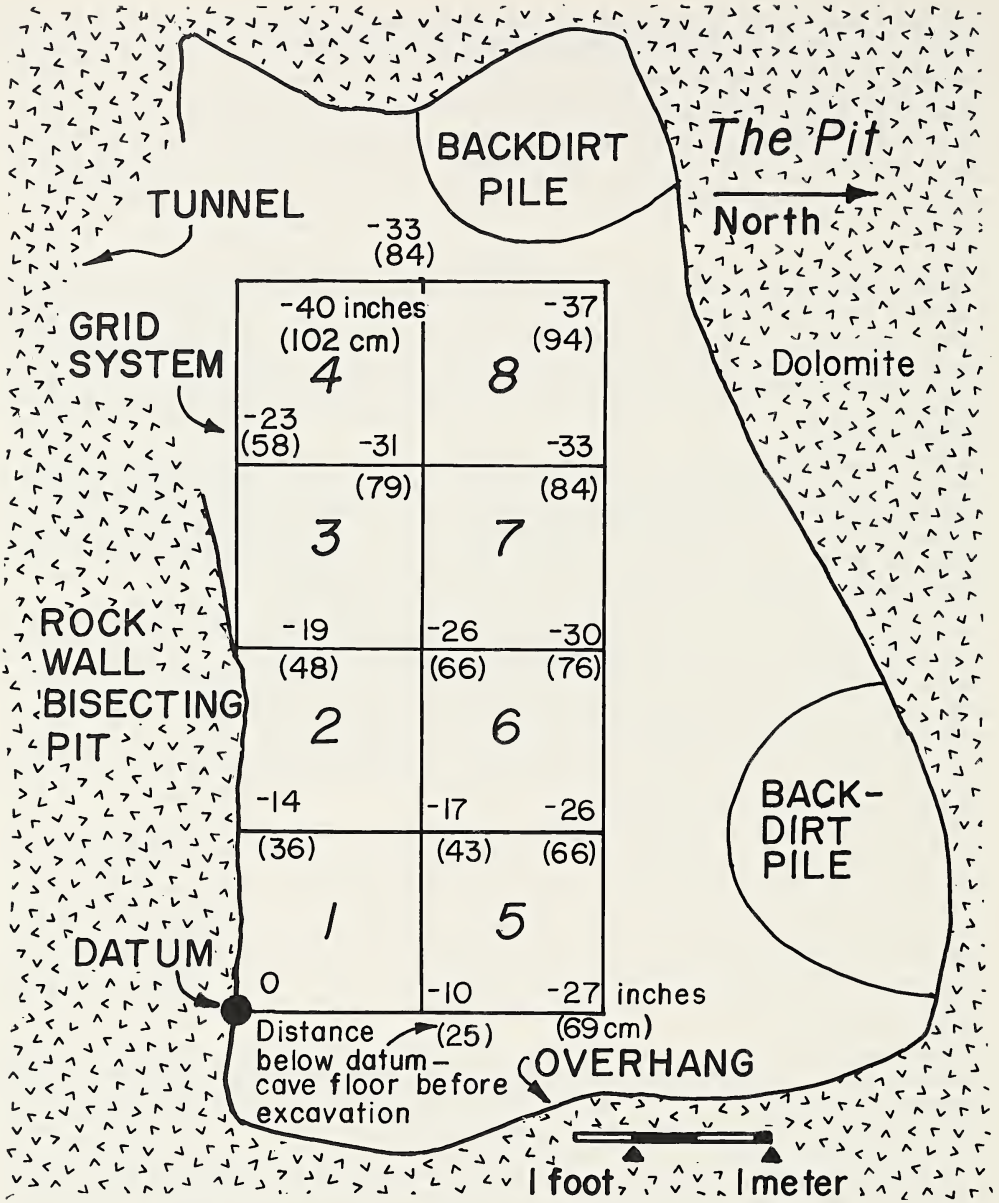


Fig. 2.—Location of excavation grids in The Pit (CM loc. 1925).

minimum distance across the constriction separating primary wings from secondary wings. *Cxpw*, minimum distance from anterior margin of lingual reentrant angle 3 to posterior margin of buccal reentrant angle 3. *C56*, minimum distance across the constriction between triangle 5 and triangle 6. *ka*, thousand years before present. *L*, maximum length at occlusal surface. *LRA*, lingual reentrant angle. *n*, number of specimens. *PCGR*, Porcupine Cave Gypsum Room. *PCVR*, Porcupine Cave Velvet Room. *PCUN*, Porcupine Cave Undifferentiated locality. *PIT*, Porcupine Cave Pit. *PL*, posterior loop. *PW*, primary wing. *R*, minimum distance from the apex of buccal reentrant 1 to lingual reentrant 1. *SD*, standard deviation. *SW*, secondary wing. *T*, triangle. *W*, width perpendicular to length. *Wac*, maximum width across anterior cap. *WP*, maximum width from the apex of triangle 1 to a line tangent to the apex of triangle 2 and parallel with the long axis of the tooth. *Wpw*, maximum

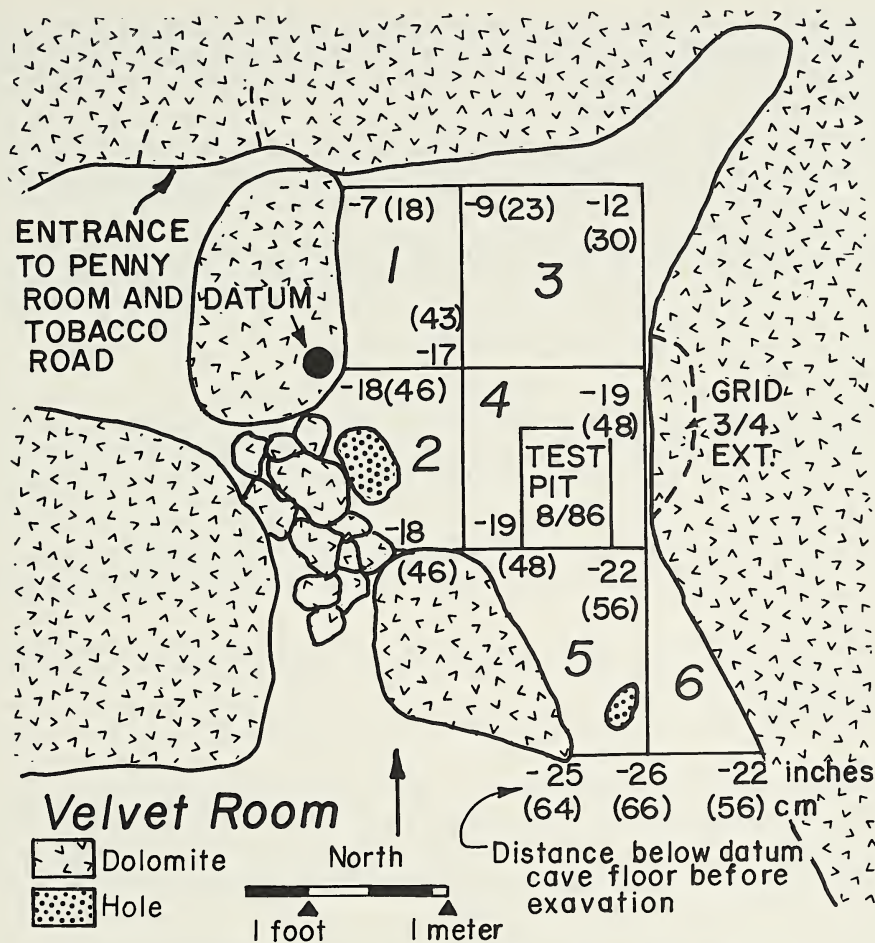


Fig. 3.—Location of excavation grids in the Velvet Room (CM loc. 1927).

width across primary wings. W_{sw} , maximum width across secondary wings. W_{12} , maximum distance from apex of triangle 1 to apex of triangle 2. W_{23} , maximum distance from apex of triangle 2 to apex of triangle 3. W_{34} , maximum distance from apex of triangle 3 to a line tangent to triangle 4 and parallel to the long axis of the tooth. W_{45} , maximum distance from apex of triangle 4 to apex of triangle 5. \bar{x} , mean.

RESULTS

Stratigraphy

The general sedimentary sequence in The Pit (Fig. 2) is alternating beds of loess interstratified with more consolidated beds rich in hard clay concretions. These alternations are of paleoclimatic significance: loess suggests effectively dry conditions in the cave, whereas clay concretions suggest wetter environments. The details of this sedimentary sequence are listed below, with information pertinent to interpreting the origins and intracave correlations of each bed. Data were obtained by excavating to a depth of -122 cm and sampling with a bucket auger from -123 to -236 cm. The auger hole collapsed when Bed 9 was encountered; additional sediment is present for an unknown depth below that point. All beds

excavated have yielded abundant fossil bone; in addition fossil bone was evident in bucket auger samples from Beds 4, 7, and 8. Beds are listed from top to bottom. Thicknesses for Beds 2 to 9 were taken in the northwest corner of Grid 2 (Fig. 2).

Bed 1. Loess, 10 YR 5/4 (moderate yellowish brown). Distributed in a cone that is 81 cm thick at the southeast corner of Grid 1 and tapers to 5 cm thick approximately 2 m to the northwest. Very soft. Comprises PIT Levels 1 through 3; 0 cm at the southeast corner of Grid 1 to -76 cm at the northwest corner of Grid 2.

Bed 2. Consolidated clay, 10 YR 4/2 (dark yellowish brown). Upper 15 cm composed of clay concretions averaging 2 to 5 cm in diameter, grading downward to concretions averaging 1 cm in diameter. Distributed in cone that is thickest in the vicinity of Grid 3 (63 cm) and tapers to the north, east, and west. Moderately hard. Comprises PIT Levels 4 and 5; -76 to -139 cm.

Bed 3. Partial pavement of rock interspersed with material that makes up Bed 2. Very hard. Thickness 6 cm (from -140 to -146 cm).

Bed 4. Clay concretions <1 cm in diameter forming soft layer from -147 to -151 cm. Dust of same material forming very soft layer from -152 to -183 cm, but more indurated medium hard layer from -184 to -200 cm. 10 YR 4/2 (dark yellowish brown). Total thickness 53 cm.

Bed 5. Mixture of brown (10 YR 4/2) and white dust, very hard. Thickness 10 cm (from -201 to -211 cm).

Bed 6. Predominantly white (N9) gypsum crystals and white dust, with minor amounts of dark yellowish brown dust. 10 YR 4/2. Soft. Thickness 9 cm (from -212 to -221 cm).

Bed 7. Brown clay (10 YR 4/2) concretions and silt averaging 1 or 2 cm in diameter mixed with white dust. Hard. Thickness 7 cm (from -222 to -229 cm). Concretions probably contamination from auger-hole wall.

Bed 8. Predominantly brown (10 YR 4/2) clay concretions of <1 cm diameter; less white dust than in Bed 7. Hard. Thickness 4 cm (from -230 to -234 cm). Concretions probably contamination from auger-hole wall.

Bed 9. Gray-brown (5 YR 3/2) oxidized clay. Hard. Thickness at least 1 cm (from -235 to -236 cm).

In the Velvet Room (Fig. 3) approximately 65 cm of sediment was excavated before bedrock was encountered. Generally these sediments resembled Bed 1 in The Pit. However, in the Velvet Room the upper 3 cm of the dust forms a mildly indurated crust and minor lithologic criteria provide additional bases for dividing it into the following excavation levels.

VR Level 1. Crust of slightly consolidated dust with abundant dried fecal pellets of rodents. 10 YR 5/4 (moderate yellowish brown). Approximately 3 cm thick.

VR Level 2A. Loose dust with sparse dried fecal pellets of rodents. 10 YR 5/4. 5 to 10 cm thick.

VR Level 2B. Moderate brown dust (5 YR 4/4) with upper and lower margin defined by white bands that resemble volcanic ash. Rodent-sized fecal pellets abundant. 10 to 15 cm thick.

VR Level 2C. Similar to VR Level 2A. 15 to 20 cm thick.

VR Level 3. Consolidated grayish-orange (10 YR 7/4) powdery material that bears the molds of rodent fecal pellets, locally grades downward into loose white dust. 18 to 30 cm thick.

VR Level 4. Similar to VR Level 3, except containing abundant pebbles, small rocks, and bone tightly cemented together. Forms 1-5 cm thick crust on underlying bedrock.

Deposits in the Ferret Room are very thin and like those of the Velvet Room resemble Bed 1 in The Pit; hence we speculate that sediments in these three areas are roughly coeval. Sediments in the Gypsum Room, Damp Room, and Badger Room in contrast are possibly older, because they are similar to Bed 2 in The Pit in being moderately consolidated nodular brown clay exceeding 1 m in thickness. However, the nodules in the Gypsum, Damp, and Badger Rooms are not as well developed as in The Pit, and the color is less yellowish, being 5 YR 3/4 (moderate brown) for the Gypsum and Damp Rooms and 5 YR 4/4 (moderate brown) for the Badger Room.

Fauna

Fossils are extremely abundant in The Pit, the Gypsum Room, the Velvet Room, and the Badger Room, as well as being sparsely present in most other

rooms of Porcupine Cave. The faunal analysis reported here is restricted to a small sample of specimens mostly from The Pit. Work on the rest of the fauna (Table 2) continues and will be documented in forthcoming publications.

Species of especial interest at Porcupine Cave include the arvicolines *Pitymys meadensis*, *Lagurus curtatus*, *Microtus paroperarius*, a *Microtus* species that appears to be either *montanus* or *longicaudus*, *Ondatra* cf. *annectens*, and *Mictomys* near *meltoni*. All of these except *L. curtatus* and *M. montanus/longicaudus* are extinct. The association of these six species has not been reported elsewhere and has biostratigraphic as well as paleoenvironmental significance. Identifications were based on the following criteria.

Pitymys meadensis

Specimens, Localities, and Levels.—Specimens from The Pit (PIT), CM loc. 1925, include CM 45402–45405, 45428–45430 (5 left and 2 right M_1 s), CM 45406–45408 (1 left and 2 right M^3 s) from PIT Level 1; CM 45431–45447 (4 left and 13 right M_1 s) from PIT Level 2.

Specimens from the Gypsum Room (PCGR), CM loc. 1926, include CM 45424 (right jaw with M_1 and M_2), CM 45425–45427 (3 right M^3 s).

Specimens from undifferentiated localities in Porcupine Cave (PCUN), CM loc. 1932, include CM 45448 (right jaw with I- M_1) and 45449–45453 (2 left and 3 right M_1 s), CM 45454–45456 (1 left and 2 right M^3 s).

Identification and Comparisons.—We follow Zakrzewski (1985) and Repenning (1983) in considering *Pitymys* to be of generic rank. All *Pitymys* species are characterized by an anteroconid complex on M_1 that consists of pairs of confluent triangles, with the individual triangles of each pair sharing a common base (Fig. 4a, 5a). In contrast all *Microtus* species are characterized by an anteroconid complex that has alternating triangles (Fig. 6b, 7b). This morphological difference warrants a generic distinction (*contra* Martin, 1987:276), because it is greater than that exhibited among species within either *Pitymys* or *Microtus*. Moreover it is more pronounced and consistent than the differences in occlusal pattern that distinguish between first lower molars of other arvicoline genera, for example *Lagurus* (Fig. 4b, 5b) and *Microtus* (Fig. 6b, 7b). For convenience we follow Martin (1987) in considering species commonly referred to the subgenera *Pedomys* and *Herpetomys* to be included within *Pitymys*, although until more evidence becomes available we reserve judgement as to the details of the phylogenetic relationships among these three groups.

Like other specimens of *Pitymys meadensis*, the M_1 s from Porcupine Cave have an anteroconid complex characterized by broadly confluent well developed primary wings that are separated from moderately well developed confluent secondary wings by the very deep buccal reentrant 3 and lingual reentrant 4 (Fig. 4a, 5a). These two reentrants are in such close proximity that they nearly touch as is common in *P. meadensis*, *P. aratai*, *P. quasiater*, *P. guatemalensis*, *P. oaxacensis*, *P. nemoralis* (= [*P.*] *pinetorum nemoralis* of Martin, 1987), and in the very few specimens that represent *P. mcnowni*. Only infrequently is this condition observed in *P. ochrogaster*, which may be a senior synonym of *P. mcnowni* (Martin, 1987). The Porcupine Cave specimens resemble *P. meadensis* in having a relatively long narrow anterior cap that is consistently well demarcated from the secondary wings by constriction between buccal reentrant 4 and a particularly deep lingual reentrant 5. This distinguishes the Porcupine Cave material from *P. aratai*, *P. guatemalensis*, and the vast majority of *P. nemoralis* and *P. ochrogaster* specimens, which are characterized by weaker development of the secondary wings and consequently less obvious separation of a shorter rounder anterior cap. Like *P. meadensis*, the Porcupine Cave specimens differ from *P. quasiater* in having a relatively

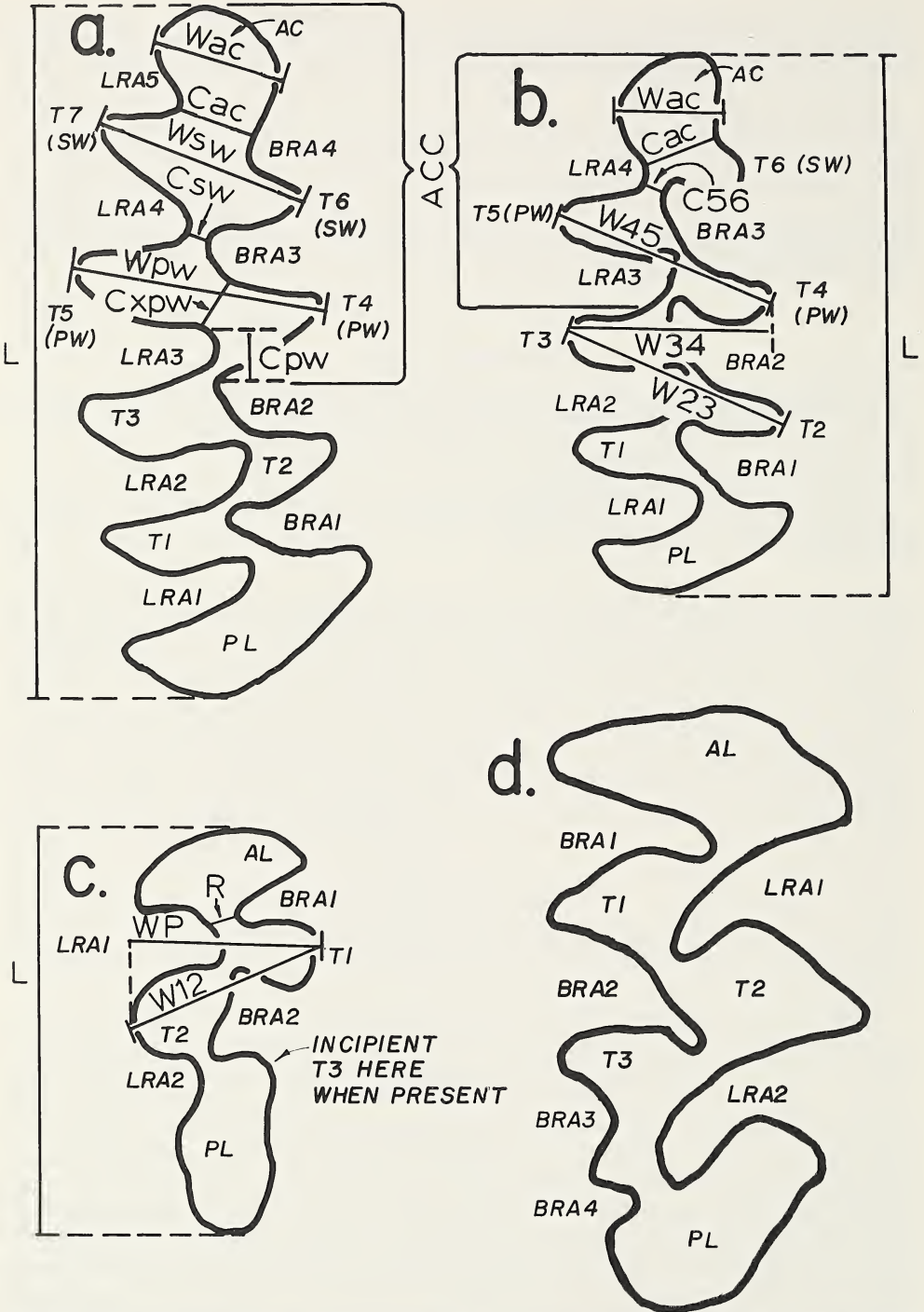


Fig. 4.—Dental terminology and measurements for: a, *Pitymys meadensis* right M_1 ; b, *Lagurus curtatus* right M_3 ; c, *Lagurus curtatus* left M^3 ; and d, *Ondatra* cf. *annectens* right M^3 . See text for further explanation of measurements and abbreviations.

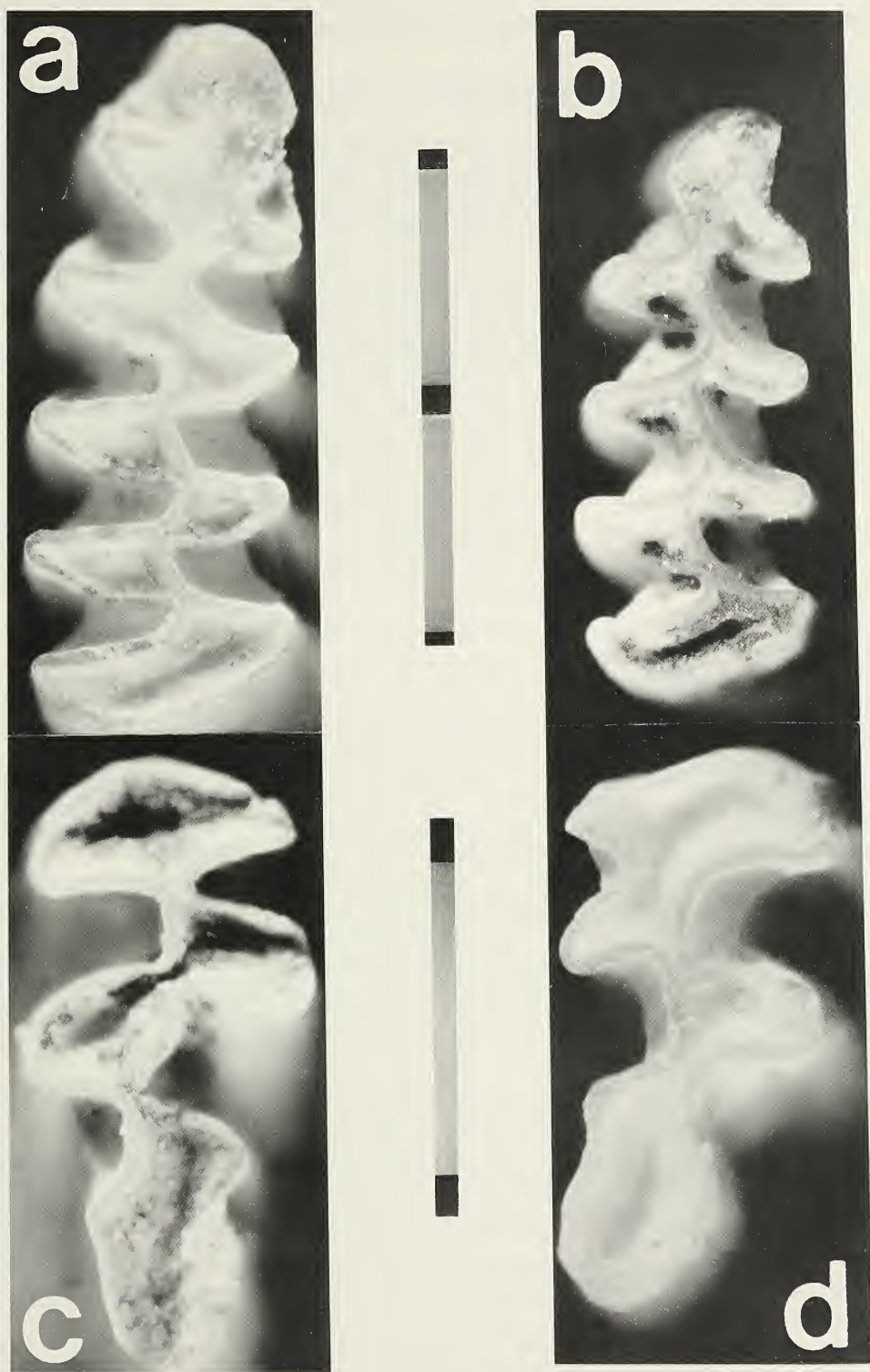


Fig. 5.—Fossil microtine teeth from Porcupine Cave: a, CM 45439, *Pitymys meadensis* right M_1 from PIT Level 2; b, CM 45471, *Lagurus curtatus* right M_1 from PIT Level 3; c, CM 45480, *L. curtatus* left M^3 from PCUN (note deep BRA1); d, CM 45410, *L. curtatus* right M^3 from PIT Level 1 (note shallow BRA1). Upper scale bar for a and b is 2 mm long; lower scale bar for c and d is 1 mm long.

longer narrower anterior cap and broad reentrants that do not curve anteriorly (Martin, 1987).

The M_2 s from Porcupine Cave have triangle 3 completely separated from triangle 4. This condition is characteristic of *P. meadensis* (Hibbard, 1944), but not of *P. quasiater*, *P. mcnowni* (if indeed this is a valid species), *P. ochrogaster*, and *P. nemoralis* in which the two triangles generally are broadly confluent (Repenning, 1983; Martin, 1987).

The Porcupine Cave M^3 s have a simple posterior loop and only 2 lingual reentrants like *Pitymys meadensis* (Rensberger et al., 1984:fig. 11; Repenning, 1983). In contrast, M^3 in *P. oaxacensis* and *P. guatemalensis* has additional lingual projections on the posterior loop, which result in 3 or 4 lingual reentrants (Martin, 1987:figs. 2E, 7B).

P. meadensis is known elsewhere in Colorado from Hansen Bluff approximately 180 km south of Porcupine Cave (Rogers et al., 1985). The species also occurs in faunas from Cudahy, Meade County, Kansas, which is the type locality (Hibbard, 1944; Paulson, 1961); Tobin, Kansas (Repenning, 1983); Kennewick, Benton County, Washington (Rensberger et al., 1984); North Livermore Avenue, Alameda County, and Olive Dell Ranch near Los Angeles, California (Repenning, 1983); and possibly El Tajo de Tequixquiac, Mexico (Repenning, 1983; Martin, 1987, disputes this identification).

Comparisons by t-tests ($P < 0.05$) of all possible pairs of M_1 samples from Kennewick, Cudahy, and each locality and level in Porcupine Cave showed few statistically significant differences (Table 3): (1) the teeth are shorter [measurement L, Fig. 4a] in PIT Level 2 specimens than in Kennewick specimens; (2) the primary wings are narrower [measurement Wpw] in PIT Level 2 specimens than in Kennewick specimens, and wider in the single PCGR specimen as compared to the Cudahy sample; (3) the secondary wings are wider [measurement Wsw] in the PCGR and PCUN samples than in the Cudahy sample; (4) the anterior cap [measurement Wac] is wider in PIT Level 2 specimens than those from PIT Level 1, from Kennewick, and like the PCGR sample also wider than in specimens from Cudahy; (5) triangle 5 is positioned more anterad in respect to triangle 4 [measurement Cpw] in the PIT Level 1 sample than in the Kennewick sample, and in the PCUN sample as compared to the Kennewick and Cudahy samples; and (6) the constriction between the primary wings and secondary wings [measurement Csw] is more pronounced in specimens from PIT Level 2 and Kennewick than those from PCGR or PCUN, and more pronounced in specimens from Cudahy than in those from PCGR.

This series of measurements shows that at least some of the Porcupine Cave samples differ from specimens from the type locality of *P. meadensis* in being wider across the primary wings (PCGR), wider across the secondary wings (PCGR and PCUN), wider across the anterior cap (PCGR and PIT Level 2), having the lingual primary wing positioned more anterad (PCUN), and in the less pronounced constriction between the primary and secondary wings (PCGR). Kennewick samples do not differ significantly from the available Cudahy samples in any measurements discussed above, yet they do differ in minor attributes from some of the Porcupine Cave samples.

However, the differences between the samples from Porcupine Cave and those from other localities are not of a magnitude that would preclude assigning the Porcupine Cave specimens to *P. meadensis*. Extant species of microtines that show as much or more intraspecific dental variation include for example *Pitymys guatemalensis*, *P. ochrogaster* (Martin, 1987), *Microtus pennsylvanicus* (personal

Table 3.—Measurement (mm) statistics for *M.* of *Pitymys meadensis*. See text and Figure 4 for explanation of abbreviations and measurements.

	L	Wpw	Wsw	Wac	Cpw	Cxpw	Csw	Cac	n	Locality
\bar{x}	3.007	1.025	0.857	0.438	0.201	0.223	0.055	0.312	6	PIT 1
SD	0.147	0.057	0.053	0.091	0.036	0.023	0.019	0.066		
Low	2.80	0.96	0.80	0.32	0.13	0.20	0.03	0.24		
High	3.17	1.11	0.93	0.54	0.23	0.26	0.08	0.40		
\bar{x}	2.946	1.032	0.858	0.522	0.177	0.207	0.052	0.270	16	PIT 2
SD	0.131	0.049	0.059	0.060	0.061	0.054	0.013	0.082		
Low	2.84	0.97	0.75	0.44	0.08	0.13	0.02	0.11		
High	3.23	1.12	0.95	0.64	0.31	0.28	0.08	0.39		
\bar{x}	3.023	1.066	0.896	0.486	0.224	0.189	0.073	0.295	6	PCUN
SD	0.185	0.063	0.049	0.088	0.017	0.021	0.025	0.077		
Low	2.81	0.96	0.82	0.38	0.20	0.15	0.05	0.16		
High	3.25	1.12	0.95	0.62	0.24	0.22	0.12	0.38		
45424*	3.02	1.12	0.96	0.52	0.22	0.18	0.09	0.31	1	PCGR
\bar{x}	3.081	1.076	0.883	0.470	0.151	0.241	0.047	0.272	29	Kennewick
SD	0.207	0.070	0.073	0.076	0.050	0.046	0.020	0.089		
Low	2.77	0.89	0.71	0.30	0.05	0.15	0.02	0.08		
High	3.41	1.18	1.05	0.58	0.25	0.34	0.07	0.46		
7480*	2.86	0.99	0.83	0.35	0.20	0.23	0.05	0.42	1	Cudahy
7481*	2.69	0.98	0.78	0.41	0.15	0.27	0.05	0.36	1	Cudahy

*CM Specimen number.

observations), *M. xanthognathus*, *M. chrotorhinnus* (Guilday, 1982), *M. arvalis* (Corbet, 1986), and *Clethrionomys glareolus* (Kowalski, 1970; Corbet, 1975).

Like the intraspecific variation in these extant voles, the morphological distinctiveness among the different samples of *P. meadensis* probably reflects population-level differences induced by biogeographic or temporal separation. This postulate is consistent with the observation that the two Colorado samples—Porcupine Cave and Hansen Bluff—share a character not found in two of the West Coast samples, which consist of two teeth from North Livermore Avenue, California and more than 50 teeth from Kennewick, Washington. In the Colorado specimens, the apex of the reentrants separating the primary and secondary wings forms a more open angle than in the West Coast specimens.

The only statistically significant difference among samples within The Pit is a change from a relatively wide anterior cap in PIT Level 2 to a narrow cap in the superjacent PIT Level 1 [measurement Wac, Table 3]. This is accompanied by apparent (but statistically nonsignificant) anterad migration of triangle 5 relative to triangle 3 [increase in measurement Cpw] and opening of the constriction between the secondary wings and anterior cap [increase in measurement Cac]. These differences may indicate random fluctuation of morphology through time or response to environmental changes between PIT Levels 1 and 2, a possibility considered in more detail in the Discussion.

A statistically significant difference in constriction between the primary and secondary wings [measurement Csw] also is evident in comparing specimens from PIT Level 2 with those from PCGR and PCUN. The PIT Level 2 specimens show more constriction than those from the other two localities.

Lagurus curtatus

Specimens, Localities, and Levels.—Specimens from The Pit (PIT), CM loc. 1925, include CM 45457 (left jaw with I-M₁), CM 45458 (right jaw with I-M₂), CM 45459 and 45465 (2 right jaws with

Table 4.—Measurement (mm) statistics for *M₁* of *Lagurus curtatus*. See text and Figure 4 for explanation of abbreviations and measurements.

	L	W23	W34	W45	C56	Cac	WAC	n	Locality
\bar{x}	2.701	1.099	0.990	1.037	0.073	0.197	0.585	13	Modern†
SD	0.088	0.051	0.044	0.067	0.039	0.082	0.066		
Low	2.57	1.02	0.93	0.91	0.03	0.06	0.45		
High	2.83	1.22	1.01	1.19	0.19	0.35	0.68		
\bar{x}	2.498	0.979	0.892	0.948	0.089	0.253	0.403	6	PIT 1
SD	0.116	0.061	0.050	0.051	0.060	0.021	0.070		
Low	2.42	0.88	0.80	0.92	0.02	0.23	0.33		
High	2.65	1.07	0.95	1.01	0.16	0.29	0.52		
45466*	2.63	1.03	0.94	0.94	0.26	0.24	0.47	1	PIT 2
45467*	2.38	0.95	0.86	0.87	0.25	0.27	0.41	1	PIT 2
\bar{x}	2.50	0.998	0.894	0.964	0.106	0.260	0.430	5	PIT 3
SD	0.158	0.031	0.075	0.081	0.073	0.045	0.081		
Low	2.31	0.96	0.83	0.92	0.04	0.22	0.37		
High	2.75	1.05	1.02	1.11	0.23	0.32	0.57		
45478*	2.68	1.05	0.88	1.01	0.06	0.22	0.52		
45475*	2.18	0.85	0.79	0.83	0.17	0.18	0.33	1	PCGR
45476*	2.18	0.78	0.75	0.82	0.15	0.24	0.51	1	PCGR

* CM Specimen number.

† 12 specimens from Fremont County, Wyoming and 1 specimen from Malheur County, Oregon.

M_1 - M_2), CM 45460–45464 (3 left and 2 right M_1 s), CM 45410–45413 (2 left and 2 right M^3 s) from PIT Level 1; CM 45466–45467 (2 right M_1 s) from PIT Level 2; CM 45468–45472 (2 left and 3 right M^3 s) from PIT Level 3; CM 45473 (left M^3), CM 45474 (left M_2) from PIT Level 5.

Specimens from the Gypsum Room (PCGR), CM loc. 1926, include CM 45475–45476 (2 left M_1 s).

Specimens from the Velvet Room (PCVR), CM loc. 1927, include CM 45477 (skull with M^2) from PCVR Unknown Level; CM 45478 (right M_1), CM 45479 (left M^2).

Specimens from undifferentiated localities in Porcupine Cave (PCUN), CM loc. 1932, include CM 45480–45481 (1 left and 1 right M^3).

Identifications and Comparisons.—Teeth of these voles are recognizable as *Lagurus curtatus* because, unlike the condition in other lagurines, they have cement in the reentrants (Carroll and Genoways, 1980; Hall, 1981). Also the M^3 has a long posterior loop lacking a pronounced anterobuccal projection in the region of triangle 3; therefore only two triangles are present between the posterior and anterior loops and these are poorly developed (Fig. 4c, 5c, d). M^3 s in other species of *Lagurus* and *Prolagurus* have an anterobuccal projection on the posterior loop, which gives the appearance of at least an incipient triangle (T3) posterior to the two well developed ones between the posterior and anterior loops (T1 and T2) (Chaline, 1985:636). M^2 s from Porcupine Cave are assigned to *L. curtatus* on the basis of the anteroposteriorly expanded lingual reentrant, which makes the lingual border of triangle 1 long and almost aligned with the long axis of the tooth. M_1 s are recognizable in part by their anteroconid complex on which triangles 4 and 5 are moderately well developed and alternating, triangle 6 is obvious but confluent with a relatively simple anterior cap, and triangle 7 is absent. M_1 s with this type of anteroconid complex were referred to *L. curtatus* only if they also had relatively expanded reentrant angles and rounded salient angles, narrow triangle bases, and a triangle 2 that is subequal in size to or larger than triangle 1 (Fig. 4b, 5b).

Within The Pit locality, the sample from Level 2 differs significantly (t-test, 0.05 level) from those of Levels 1 and 3 in less constriction between T5 and T6 [larger measurement C56, Fig. 4b]. The Level 3 sample is significantly less con-

Table 5.—Measurements (mm) for *M*³ of *Lagurus curtatus*. See text and Figure 4 for explanation of abbreviations and measurements.

CM no.	L	W12	WP	R	Locality
G970-1	1.79	0.98	0.97	0.02	Modern, Fremont County, Wyoming
G970-3	1.85	0.95	0.92	0.03	
G970-4	1.78	0.80	0.80	0.01	
G970-6	1.78	0.88	0.81	0.04	
G970-10	1.89	0.97	0.92	0.03	
G818	1.60	0.80	0.75	0.06	Modern, Malheur County, Oregon
45410	1.58	0.71	0.70	0.17	
45411	1.53	0.75	0.71	0.06	
45412	1.54	0.69	0.66	0.10	
45473	1.57	0.69	0.64	0.13	
45480	1.71	0.78	0.74	0.03	
45481	1.66	0.79	0.74	0.13	

stricted than the Level 1 sample. The PIT Level 2 sample also differs from the PCGR sample in this respect (Table 4).

*M*₁s from PCGR appear smaller [measurements L and W23, Fig. 4b] than those of all PIT levels, but the size difference is statistically significant only in comparison to teeth from PIT Levels 1 and 3.

Fossils of *L. curtatus* have not been reported from elsewhere in Colorado but are known from Idaho (Jaguar, Moonshiner, and Wasden Caves), Wyoming (Bell, Horned Owl, and Little Box Elder Caves), Montana (Warm Springs and False Cougar Cave), New Mexico (Isleta and Dry Caves), and Washington (Kennewick) (Kurtén and Anderson, 1980; Rensberger et al., 1984; Bonnicksen et al., 1986). The specimens from Porcupine Cave are most similar to those from the lowest stratigraphic levels at Kennewick in that the majority of *M*³s (71% at Porcupine Cave) have a very shallow buccal reentrant 1 (Fig. 5d), so that triangle 1 is widely confluent with the anterior loop (Rensberger et al., 1984; Barnosky, 1987). In contrast, most other samples of *L. curtatus* are characterized by an *M*³ with a deep anterobuccal reentrant that completely separates triangle 1 from the anterior loop (Carroll and Genoways, 1980:fig. 1). This applies to modern specimens from at least Wyoming, Washington, and Oregon, as well as to fossils from the upper stratigraphic levels at Kennewick.

The Porcupine Cave fossils are statistically different, as determined by t-tests ($P < 0.05$), from a modern sample of *Lagurus curtatus* in the following ways (Tables 4, 5): (1) smaller size [on *M*₁ measurement L, W23, W34, W45; on *M*³ measurement L, W12, WP]; (2) less constriction between T6 and the anterior cap in samples from PIT Levels 1 and 3 [ratio $Cac/L \times 100$]; (3) narrower anterior cap in PIT Levels 1, 2, and 3 [ratio $Wac/L \times 100$], which reflects the absence of an incipient triangle 7; and (4) shallower buccal reentrant 1 on *M*³ [measurement R and ratio $R/L \times 100$]. The last three of these differences may prove to be markers of primitive morphology in populations of *Lagurus curtatus*, in view of their presence in the lower (but not the upper) stratigraphic levels at Kennewick as well as throughout Porcupine Cave. In all four of these features, however, there is morphological overlap between the fossil and recent samples, and the differences are less than the interpopulation variation that has been noted for species of *Pitymys*, *Microtus* and *Clethrionomys*. Hence, even the most important of the differences—fossil *M*³s with shallower buccal reentrant 1—would not provide a

Table 6.—Measurements (mm) for *M₁* of *Microtus paroperarius*. Length and width are maxima taken at occlusal surface.

CM no.	Length	Width	Locality
45482	2.64	0.99	PIT 2
45483	2.62	0.99	PIT 2
45484	2.66	0.95	PIT 2
45506	2.54	0.92	PIT 3
45507	2.59	1.07	PIT 3

valid criterion to erect a new species for the Porcupine Cave material in the absence of a prolonged study of variation among modern *Lagurus curtatus*.

Microtus paroperarius

Specimens, Localities, and Levels.—All specimens are from The Pit (PIT), CM loc. 1925. CM 45482–45484 (2 left and 1 right *M₁*s) from PIT Level 2; CM 45506–45507 (2 left *M₁*s) from PIT Level 3.

Identification and Comparisons.—In all of their characteristics the *M₁*s from Porcupine Cave fall well within the variation exhibited in the large samples of *Microtus paroperarius* from Cumberland Cave in Maryland (van der Meulen, 1978) and from the Sunbrite Ash Mine (Cudahy fauna) in Kansas, which is the type locality (Hibbard, 1944; Paulson, 1961). The characteristics of *M₁* that define the species are evident: four closed alternating triangles, triangle 5 opening broadly into the anterior cap that may include weakly developed triangles 6 and 7, and cement in lingual reentrant angle 4 in at least 60% of the specimens (Hibbard, 1944; Paulson, 1961; van der Meulen, 1978; Zakrzewski, 1985). However, with a length averaging 2.61 mm (Table 6) the Porcupine Cave specimens are shorter than measurements published for other samples. *M₁*s from nearby Hansen Bluff average 3.50 mm in the lower part of the section and 2.90 mm in the upper part (Rogers et al., 1985:552). Samples from the Cudahy fauna measured by Rogers et al. (1985:552) also average 2.90 mm in length, but topotypic material from the Sunbrite Ash Mine measured by van der Meulen (1978:121) is slightly smaller, averaging 2.79 mm. These slightly smaller sizes also characterize teeth from Conard Fissure in Arkansas and Cumberland Cave, which average 2.73 mm and 2.74 mm, respectively (van der Meulen, 1978:121). Other localities from which *M. paroperarius* has been reported include Mullen in Nebraska; Vera in Texas; Little Sioux in Iowa; Hall Ash Pit, Tobin, Wilson Valley, and Holzinger in Kansas; Hanover Quarry Fissure in Pennsylvania; and Wellsch Valley in Saskatchewan (Kurtén and Anderson, 1980; Rogers et al., 1985; Zakrzewski, 1985).

*M₁*s of *Microtus paroperarius* from Porcupine Cave somewhat resemble those of *Lagurus curtatus* from the same deposits but can be separated on a number of criteria. In contrast to the asymmetric development of secondary wings in *M₁*s of *Lagurus curtatus* (Fig. 4b, 5b), weak secondary wings generally are developed equally on both the buccal and lingual sides of the tooth in *M. paroperarius* (Fig. 6b, 7b). Triangle 6 in *M. paroperarius* is broadly confluent with triangle 5, whereas a constriction partially or wholly separates triangle 6 from triangle 5 in *L. curtatus*. Other traits that serve to separate *M₁*s of *M. paroperarius* from those of *Lagurus curtatus* in the Porcupine Cave sample include (1) sharper salient angles; (2) reentrant angles more acute; (3) triangle bases broader; and (4) triangle 2 much smaller than triangle 1, rather than subequal in size or larger (compare Fig. 4b, 5b with 6b, 7b).

Microtus montanus or *Microtus longicaudus*

Specimens, Localities, and Levels.—All specimens are from The Pit (PIT), CM loc. 1925. CM 45485–45486, 45497–45498, 45502 (2 left and 3 right M_1 s) from PIT Level 1; CM 45487–45494, 45499 (2 left and 6 right M_1 s) from PIT Level 2; CM 45495–45496 (1 right and 1 left M_1) from PIT Level 3. CM 45500–45501, 2 right M_1 s from PIT Unknown Level.

Identification and Comparison.—These teeth are characterized by well developed primary wings that alternate to form triangles 4 and 5, marked constriction between the primary and secondary wings which results in a fully formed triangle 5, and well-developed symmetrical secondary wings that are broadly confluent with the anterior cap. The shape of the anterior cap provides a basis for dividing the sample into three variants. Variant 1 has a symmetrical anterior cap that is circular or forms an anteroposterior oriented ellipse (CM 45485–45496). In Variant 2, the anterior cap is asymmetrical, with the anteriormost portion forming a liguad hook (CM 45497–45501). The single specimen of Variant 3 (CM 45502) has a symmetrical, anteroposteriorly short anterior cap, like that commonly found in *M. pennsylvanicus*. Like Variants 1 and 2, however, Variant 3 can be distinguished from *M. pennsylvanicus* by having an expanded buccal reentrant 3, rather than an acute reentrant angle that points anterad. Such an acute, anterad-pointing buccal reentrant 3 characterizes samples of modern *M. pennsylvanicus* from central Alaska, Virginia, and Colorado. Variants 1 and 2 also differ from *M. pennsylvanicus* in having a longer narrower anterior cap. The Porcupine Cave specimens differ from the two modern specimens of *Microtus mexicanus* (CM Mammalogy 57258, 57259) that we have seen in either less closure or more offset between triangles 6 and 7. Both of the *M. mexicanus* specimens exhibit completely closed triangle 6 on the right side of the jaw, but on the left side triangles 6 and 7 are broadly confluent with their posterior borders forming a more nearly straight line than in the Porcupine Cave specimens.

The M_1 s from Porcupine Cave cannot qualitatively be distinguished from *M. montanus* and *M. longicaudus*. Because these are the only *Microtus* species besides *M. pennsylvanicus* that presently inhabit the site, the most parsimonious referral is to one of them. Nevertheless additional quantitative work, particularly discriminant analysis as applied by Smartt (1977), is needed to more rigorously compare these teeth to those of other *Microtus* with five triangles on M_1 .

M. montanus and *M. longicaudus* are represented at a number of Pleistocene and Holocene sites in the American West, including localities in Colorado, Idaho, and Wyoming (Kurtén and Anderson, 1980; Harris, 1985; Zakrzewski, 1985). However, neither species is present at Hansen Bluff.

Measurement statistics (in mm) for 17 of the Porcupine Cave specimens are: L , \bar{x} = 2.95, SD = 0.16, OR = 2.70 – 3.29; W , \bar{x} = 1.09, SD = 0.04, OR = 1.00 – 1.18.

Ondatra cf. *annectens*

Specimens, Localities, and Levels.—CM 45409, right M^3 from PIT Level 1, from The Pit, CM loc. 1925.

Identification and Comparison.—The single M^3 from Porcupine Cave resembles three specimens of *Ondatra annectens* from Cumberland Cave in the development of dentine tracts but is slightly larger (Table 7). Likewise the specimen from Porcupine Cave is larger than all five M^3 s from the lower levels of the Trout Cave Entrance Locality; these teeth were assigned by Guilday (1969, unpublished CM data) to *O. hiatidens* but later were listed as *O. annectens* (Kurtén and Anderson,

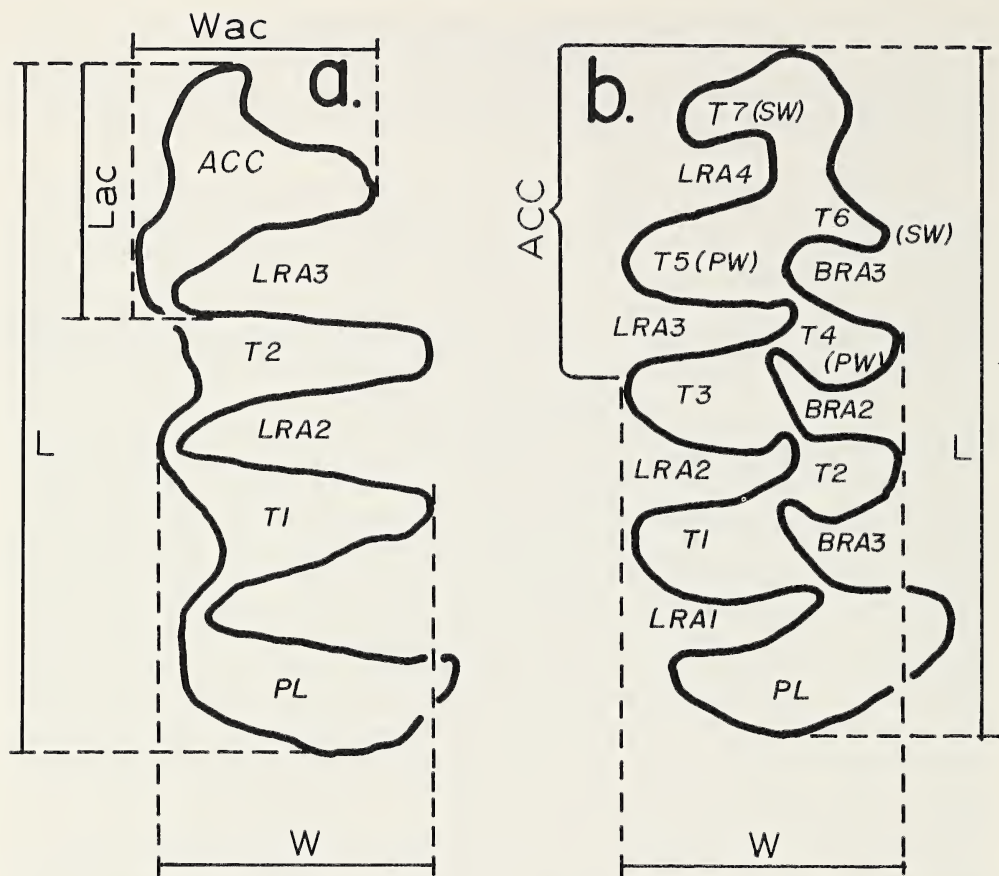


Fig. 6.—Dental terminology and measurements for: a, *Mictomys near meltoni* left M_1 ; and b, *Microtus paroperarius* right M_1 . See text for further explanation of measurements and abbreviations.

1980). Development of dentine tracts is similar in the teeth from Porcupine Cave and Trout Cave, except for those on the buccal side of the anterior loop and on triangle 1, which are nearly twice as high in the Porcupine Cave specimen than in at least 80% of the Trout Cave specimens (Table 7; Fig. 4d). The only M^3 from Hansen Bluff also differs from the Porcupine Cave specimen in having a much lower dentine tract on triangle 1; this tooth is too worn for comparison of other tracts. The M^3 from Porcupine Cave differs from most specimens of *O. annectens* in having an extra crenulation (BRA4 in Fig. 4d) that extends along the entire buccal side of the posterior loop; for this reason assignment to the species is tentative.

Mictomys near meltoni

Specimens, Localities, and Levels.—All specimens are from The Pit (PIT), CM loc. 1925. CM 45414 (right jaw with I- M_2), 45415–45416 (2 left and 1 right M_1 s), 45418–45419 (1 right and 1 left M^3) from PIT Level 1; CM 45509–45510 (2 right M_1 s) from PIT Level 2; CM 45511 (right M^3) from PIT Level 5.

Description and Comparison.—Like other specimens assigned to *Mictomys* (von Koenigswald and Martin, 1984), the M_1 s from Porcupine Cave are composed of

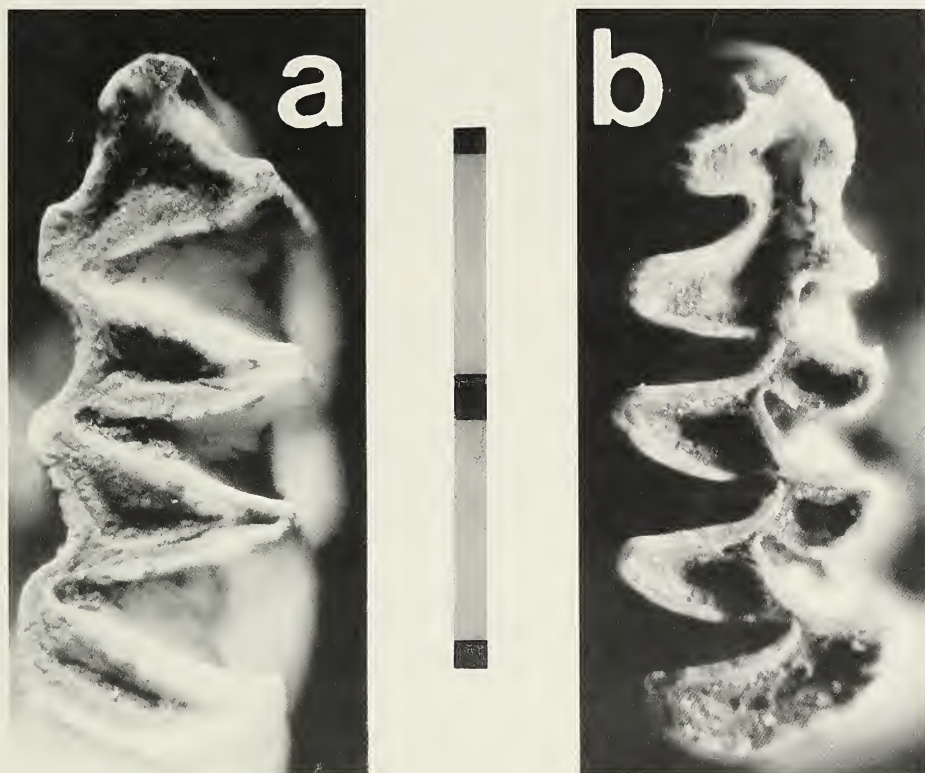


Fig. 7.—Fossil microtine teeth from Porcupine Cave: a, CM 45416, *Mictomys* near *meltoni* left M_1 from PIT Level 1; b, CM 45484, *Microtus paroperarius* right M_1 from PIT Level 2.

a series of triangles that share the same buccal baseline, rather than alternating triangles (Fig. 6a, 7a). The Porcupine Cave material differs from species in the subgenus *M.* (*Metaxyomys*) in the extremely shallow buccal reentrants. The single jaw from Porcupine Cave indicates that the posterior end of the lower incisors terminates anterior to M_3 , thus precluding its assignment to the subgenus *M.* (*Kentuckomys*); however breakage prohibits certain recognition of this feature. The probable anterior position at which the posterior end of the incisor terminates coupled with the shallow buccal reentrants suggest referral to *M.* (*Mictomys*). Using these criteria and the pattern of enamel prisms (*Schmelzmuster*), the only species von Koenigswald and Martin (1984) place in *Mictomys* (*Mictomys*) are extant *M. borealis* and extinct *M. meltoni*. *M. meltoni* is known mainly from the Cudahy fauna of Kansas. The Porcupine Cave material, like *Mictomys meltoni*, differs from *M. borealis* in having the enamel band on the posterior side of the triangles much thinner than enamel on the anterior side (= positive enamel differentiation of Martin, 1987) (Fig. 7a). In *M. borealis* enamel thickness is more uniform. The Porcupine Cave material also more closely resembles *M. meltoni* in the shape and proportions of the anteroconid complex, which measures approximately the same distance both anteroposteriorly and transversely, and in shape and proportions of the triangles, which are relatively broad (Table 8). In these features the Porcupine Cave teeth cannot be distinguished from specimens from Hansen Bluff, Cumberland Cave, or Snowville, Utah. The Hansen Bluff

Table 7.—Measurements (mm) for *M*³ of *Ondatra* cf. *annectens* from Porcupine Cave and referred specimens of *O. annectens* from other localities. Explanation of measurements: L, maximum length at base of tooth. W, maximum width at occlusal surface. LAL, maximum height of dentine tract on lingual side of anterior loop, measured from enamel border at base of lingual reentrant 1. T2, maximum height of dentine tract on Triangle 2, measured from enamel border at base of lingual reentrant 2. BAL, maximum height of dentine tract on buccal side of anterior loop, measured from enamel border at base of buccal reentrant 1. T1, maximum height of dentine tract on Triangle 1, measured from enamel border at base of buccal reentrant 1. T3, maximum height of dentine tract on Triangle 3, measured from base of buccal reentrant 2.

CM no.	L	W	LAL	T2	BAL	T1	T3	Locality
45049	3.8	2.0	>4.4	1.6	4.4	3.4	2.1	PIT 1
20272	3.5	2.0	4.1	1.3	>4.4	2.5	1.6	Cumberland Cave
20031a	3.1	1.6	—	0.9	3.3	2.9	1.4	
20031b	3.5	2.0	>4.3	0.8	2.9	2.7	1.3	
20017a	3.4	2.0	3.5	1.4	1.5	1.1	1.3	Trout Cave Entrance
20017b	3.6	1.9	2.7	1.6	1.4	1.6	1.8	
20017c	3.3	1.9	3.0	1.0	2.0	1.6	1.8	
20017d	3.1	1.7	2.7	1.6	1.9	0.9	1.9	
20019	3.2	1.7	>3.1	—	>3.4	>3.4	>3.4	

specimens have been referred to *M. meltoni* (Rogers et al., 1985) and the Cumberland Cave ones to *M. sp.* (van der Meulen, 1978:132). The Snowville specimens are currently under study by C. A. Repenning.

Other Species

Besides the rodents discussed above, at least 43 other species are represented in the several thousand specimens from the Porcupine Cave deposits. Among them are such extinct and extirpated forms as *Camelops*, *Equus*, possibly *Acinonyx*, *Mustela* cf. *nigripes*, and *Sylvilagus idahoensis*. Also present are many species that live in the area today or did live there in historic time. Most of these taxa have yet to be studied in detail, but preliminary identifications are presented in Table 2.

DISCUSSION

Age of Deposits

Biostratigraphy is presently the only means of dating the deposits of Porcupine Cave. The microtine rodents *Pitymys meadensis*, *Microtus paroperarius*, *Ondatra* cf. *annectens*, and *Mictomys* near *meltoni* elsewhere occur in sites that range in age from approximately 400 ka to 880 ka (Kurtén and Anderson, 1980; Rogers et al., 1985; Repenning, 1980, 1984, 1987). The geographically closest of these sites to Porcupine Cave is Hansen Bluff 180 km to the south where all four of these species occur in proximity to the Bishop Ash, which is dated at 740 ka, and through a thick section thought to span approximately 700 ka to 880 ka (Rogers et al., 1985:560).

However, two lines of evidence indicate that the Porcupine Cave deposits are younger than the top of Hansen Bluff. First, the dentine tract on triangle 2 of the Porcupine Cave muskrat is considerably higher than in the Hansen Bluff specimen, which suggests a later stage of evolution and hence a younger geologic age (Semken, 1966; Nelson and Semken, 1970; Zakrzewski, 1974). The Porcupine Cave muskrat also has higher dentine tracts than those from the Trout Cave Entrance Locality,

Table 8.—Measurements (mm) for *M.* of *Mictomys near meltoni*. See text and Figure 6 for explanation of measurements.

CM no.	L	W	Lac	Wac	Locality
45414	2.59	0.99	0.93	0.90	PIT 1
45415	—	—	0.95	0.10	PIT 1
45416	2.62	1.05	0.95	0.93	PIT 1
45509	2.81	1.07	0.95	1.04	PIT 2
45510	—	—	0.90	0.93	PIT 2

West Virginia, which is late Irvingtonian age (Zakrzewski, 1975; Kurtén and Anderson, 1980). Second, at Porcupine Cave *Lagurus curtatus* and *Microtus montanus* or *M. longicaudus* occur in the same stratigraphic levels as the four extinct species. Elsewhere this association has not been reported, nor have *L. curtatus* and *M. montanus* or *M. longicaudus* been demonstrated to appear earlier than 400 ka. They are not present at Hansen Bluff even though sample sizes there are large and the physical setting resembles that at Porcupine Cave in being a high (2300 m) intermontane park. Neither are they present in the large sample composing the Cudahy fauna, which lies beneath an ash dated at ca. 610 ka. However, differences from the Cudahy fauna could result from biogeographic as well as temporal differences because Porcupine Cave is several hundred meters higher and 700 km to the west. At Porcupine Cave the sympatry of *Lagurus curtatus* and *Microtus montanus/longicaudus* with the four extinct arvicolines documents either (1) the oldest occurrence of *L. curtatus* and *M. montanus/longicaudus*, or (2) the latest occurrence of *P. meadensis*, *M. paroperarius*, muskrats morphologically similar to *O. annectens*, and lemmings close to *M. meltoni*, or (3) perhaps both. A situation resulting in sympatry of species that elsewhere do not temporally or geographically overlap would arise if the high Rocky Mountains in which Porcupine Cave is located provided a dispersal corridor for early immigrants or a refugium for late survivors. No matter which of these alternatives ultimately proves correct, the most logical biostratigraphic assumption is that the deposits at Porcupine Cave sample a time near the last appearance of the four extinct species and the first appearance of the two extant ones, that is, near the boundary between Irvingtonian II and Rancholabrean I land-mammal ages (Repenning, 1980, 1984, 1987). The best estimate of the isotopic age of this boundary, obtained by recognizing the stratigraphic relationship of faunas to radiometrically and paleomagnetically dated strata, is ca. 400 ka.

Evidence that the biochronologic range of *L. curtatus* should be adjusted downward and that of *P. meadensis* adjusted upward also comes from the lowest stratigraphic levels at Kennewick, where these two species occur together in strata estimated to be no older than 320 ka based on rates of calcrete formation (Rensberger et al., 1984). *L. curtatus* from these basal Kennewick deposits resembles *L. curtatus* from Porcupine Cave in the shallow reentrants on M³, but differs from demonstrably younger *L. curtatus* in this respect.

Climatic Significance

Hard oxidized clay at the base of the section (Bed 9) suggests more humid conditions than exist in the cave today. This humid environment gave way to drier times, as indicated by the overlying deposits of more loosely consolidated brown silt, clay, and white gypsum powder of Beds 5, 6, 7, and 8 (clay pellets

Table 9.—Percentages of microtine species in Levels 1 through 3 of Porcupine Cave Pit.

	<i>P. meadensis</i>	<i>M. paroperarius</i>	<i>M. mont./long.</i> ¹	<i>L. curtatus</i>	<i>M. meltoni</i>
Level:					
1	29% (7)*	0% (0)	21% (5)	38% (9)	12% (3)
2	53% (17)	9% (3)	25% (8)	6.5% (2)	6.5% (2)
3	0% (0)	22% (2)	22% (2)	56% (5)	0% (0)

* Percentages based on total number of M₁s, given in parentheses.

¹ *M. montanus/longicaudus*.

augered from Beds 7 and 8 probably are from partial collapse of a higher part of the auger hole). The clay pellets composing Beds 2 through 4 identify a return to relatively humid conditions, as their structure suggests that damp or wet cohesive clay accreted around a nucleus, possibly as the nucleus rolled along the cave floor. The thickest part of Bed 2 is 2 m west of the present shaft that leads into The Pit, suggesting that the clay pellets did not drop directly into their present position. Instead, they apparently dropped into the southern half of The Pit and then rolled through a passage that connects the northern and southern parts of the room (labelled "TUNNEL" in Fig. 2).

The uppermost sediments in The Pit—Bed 1—are markedly different from those below in being loess and apparently aeolian in origin. This loess appears to have drifted into The Pit from directly above, as indicated by the position of the thickest part of Bed 1 just below the present opening into The Pit. The change in sediment type, the onset of aeolian deposition, and the lack of any consolidation or clay pellets suggests that conditions during deposition of Bed 1 were much drier than in any preceding intervals, and probably drier than today.

The postulate of extreme aridity during deposition of Bed 1 is borne out by the fossils. Both *L. curtatus* and *Sylvilagus idahoensis* are species that presently live in regions that are drier than South Park (Hall, 1981), although both prefer habitats with moderately dense stands of *Artemisia* or other shrubs (Orr, 1940; Bailey, 1936; Carroll and Genoways, 1980; Green and Flinders, 1980).

Despite the homogeneity of sediment type throughout Bed 1, the arvicoline rodents suggest environmental fluctuations during its deposition. The percentages of *Pitymys meadensis*, *Microtus paroperarius*, *Microtus montanus/longicaudus*, *Lagurus curtatus*, and *Mictomys meltoni* relative to one another fluctuate dramatically through PIT Levels 1, 2 and 3 (Table 9). This is particularly true for *P. meadensis* and *L. curtatus*. In PIT Level 3 *L. curtatus* is the most abundant species, *P. meadensis* is absent, and *M. paroperarius* and *M. montanus/longicaudus* are equally represented. In PIT Level 2, however, *P. meadensis* becomes the most abundant species, *M. paroperarius* decreases relative to *M. montanus/longicaudus*, and *L. curtatus* all but disappears. Finally in PIT Level 1, *P. meadensis* decreases in frequency and *M. paroperarius* drops out of the record as *L. curtatus* increases.

Coincident with the fluctuating percentages of arvicoline species are changes in the M₁ of *Pitymys meadensis*. The wide anterior caps typical of PIT Level 2 give way to statistically narrower ones in PIT Level 1. Simultaneously the M₁s of *L. curtatus* change from being less constricted to more constricted in the region between triangles 5 and 6; this feature also changes significantly (from more constricted to less constricted) from Level 3 to Level 2.

In view of the fact that two of the three species that fluctuate most in abundance

are extinct it is difficult to interpret the nature of environmental changes. However the waxing and waning of *L. curtatus* probably involves availability of dense stands of *Artemisia* and *Chrysothamnus*, the presence of which correlates with its modern biogeographic range.

The combination of these data from the sedimentary record and fossil mammals suggests a succession of humid, then drier, then humid conditions through the time represented by Beds 9 to 2, followed by a much more dramatic change to very arid conditions as deposition of Bed 1 commenced. After this dramatic shift to a more arid climatic regime, two more environmental fluctuations of as yet unknown nature occurred.

The biostratigraphically inferred age of the Porcupine Cave deposits—ca. 400 ka—places it near the boundary between oxygen-isotope stages 12 and 11, which is approximately 440 ka (Bradley, 1985:185; Repenning, 1985:174). Stage 11 is an interglacial stage between the glacial stages preceding (Stage 12) and following it (Stage 10). The major environmental change at Porcupine Cave, that is, the transition from Bed 2 to Bed 1, may well record the transition from Stage 12 to Stage 11, which would indicate a relatively humid glacial followed by a dry interglacial. This seems the most reasonable assumption on the basis of available data. However, uncertainties in dating make it prudent to recognize alternative correlations, namely that the Bed 2 to Bed 1 transition corresponds to the change from Stage 11 to Stage 10 or Stage 13 to Stage 12. The environmental inference in these cases would be a wet interglacial followed by a cold dry glacial. Detailed analysis of the fauna and depositional sequence is underway to determine if one of these alternatives is more probable, or if indeed the temporal span of the deposits is even long enough to allow meaningful correlation with the oxygen-isotope curve.

CONCLUSIONS

Fossiliferous deposits at Porcupine Cave sample an interval of Pleistocene time approximately 400,000 years ago. Elsewhere in the Rocky Mountain region little paleoenvironmental information is known for this time interval. Porcupine Cave is comparable to only one other site in the Rocky Mountain states, Hansen Bluff, Colorado, in yielding extinct Pleistocene arvicoline rodents, but Hansen Bluff (ca. 700–880 ka) is considerably older. The two sites share four extinct arvicolines: *Pitymys meadensis*, *Microtus paroperarius*, *Ondatra* cf. *annectens*, and *Mictomys* near *meltoni*. However, the Porcupine Cave fauna differs from all others that have these four species in also containing the extant forms *Lagurus curtatus* and either *Microtus montanus* or *Microtus longicaudus*. Sympatry of these six species suggests that the high montane park in which Porcupine Cave is situated was a refugium for temporally late populations of the four extinct species, or part of an early dispersal corridor for the two extant ones, or both. The temporal overlap of these species suggests the date of ca. 400 ka for the Porcupine Cave deposits because elsewhere 400 ka marks the last appearance of *P. meadensis*, *M. paroperarius*, *O. annectens*, and *M. meltoni*, and is just prior to the first occurrence of *L. curtatus* and *M. montanus/longicaudus*.

The sediments in Porcupine Cave document a major environmental change from relatively humid to extremely arid conditions. If the biostratigraphic dating is reliable, this change may coincide with a glacial-interglacial transition near oxygen-isotope Stage 11. At least five potentially less pronounced environmental

fluctuations are evident from the mammal and sedimentologic data: three of these took place during the time represented by the brown silt and clay and white gypsum, and two took place during the time of aridity represented by the loess. Some of these five lower-magnitude climatic oscillations may correspond to glacial-interglacial transitions correlating with oxygen-isotope stages below Stage 11.

The concept of no-analog or "disharmonious" assemblages, hitherto recognized only in late Wisconsinan faunas, also applies to the much older Porcupine Cave fauna. Like the late Wisconsinan no-analog faunas, the Porcupine Cave fauna reveals sympatry among species that still live in the region, species whose biogeographic range presently stops short of the study site, species that in other time intervals are allopatric, and extinct species. Thus despite its alpine location at 2900 m elevation, South Park supported a rich fauna through both minor and major environmental changes in the late-middle Pleistocene.

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STEGOTRETUS AGYRUS A NEW GENUS AND SPECIES
OF MICROSAUR (AMPHIBIAN) FROM THE
PERMO-PENNSYLVANIAN OF NEW MEXICO

DAVID S BERMAN

Associate Curator, Section of Vertebrate Fossils

DAVID A. EBERTH¹

DONALD B. BRINKMAN¹

ABSTRACT

A new genus and species of tuditanomorph microsauro, *Stegotretus agyrus*, is based on a large series of specimens that includes numerous skulls with some associated postcranial skeletons. All the specimens were collected from a Permo-Pennsylvanian horizon of the Cutler Formation near Arroyo del Agua, north-central New Mexico. *S. agyrus* is the only unquestionable microsauro to be reported from New Mexico. On the basis of shared-derived characters *S. agyrus* is considered most closely related to the more specialized *Pantylus* and is assigned to Pantylidae. The family is redefined on synapomorphies uniting *S. agyrus* and *Pantylus*, and it is recommended that the poorly known *Trachystegos*, the only other genus assigned to the family, be removed as indeterminate and relegated to family *incertae sedis*. With one exception the *S. agyrus* specimens were found in association with a surface lag of caliche nodules and calcite-rich siltstone pebbles, suggesting an original association with an overbank facies. The composition and paleogeographic distribution of two discrete lithofacies assemblages in the general collecting area reinforces this interpretation. It is speculated that the *S. agyrus* specimens may represent an aestivation assemblage.

A partial lower jaw from a Lower Permian horizon of the Cutler Formation of the same area, whose only previous description has been a very brief statement of its closeness in form to *Pantylus*, is described and illustrated. A tentative assignment to Pantylidae is recommended.

INTRODUCTION

Despite approximately a century of collecting in the Permo-Pennsylvanian redbeds of New Mexico, small, salamander-like microsauro amphibians in that state have gone nearly undetected. The first record was a probable microsauro from a Lower Permian horizon of the Cutler Formation near the village of Arroyo del Agua, Rio Arriba County, in the north-central part of the state. This was briefly reported by Langston (1953, p. 360), who noted only that "a mandible of a form near *Pantylus*" was collected from the well-known Anderson quarry. Recently, Eberth and Berman (1983) reported the discovery of a concentration of microsauro remains near the well-known Camp quarry (see Langston, 1953, for description of localities) also in the Cutler Formation and near Arroyo del Agua, but from a lower horizon best considered Permo-Pennsylvanian in age (Figs. 1, 2). A few of the specimens were illustrated photographically, but a detailed description was postponed. All of the specimens, which include numerous skulls and some associated postcranial skeletons, pertain to a single new species of pantylid microsauro. It is quite distinct, however, from the possible pantylid represented by the earlier reported jaw.

¹ Address: Tyrrell Museum of Palaeontology, P.O. Box 7500, Drumheller, Alberta T0J 0Y0, Canada. Submitted 25 March 1988.

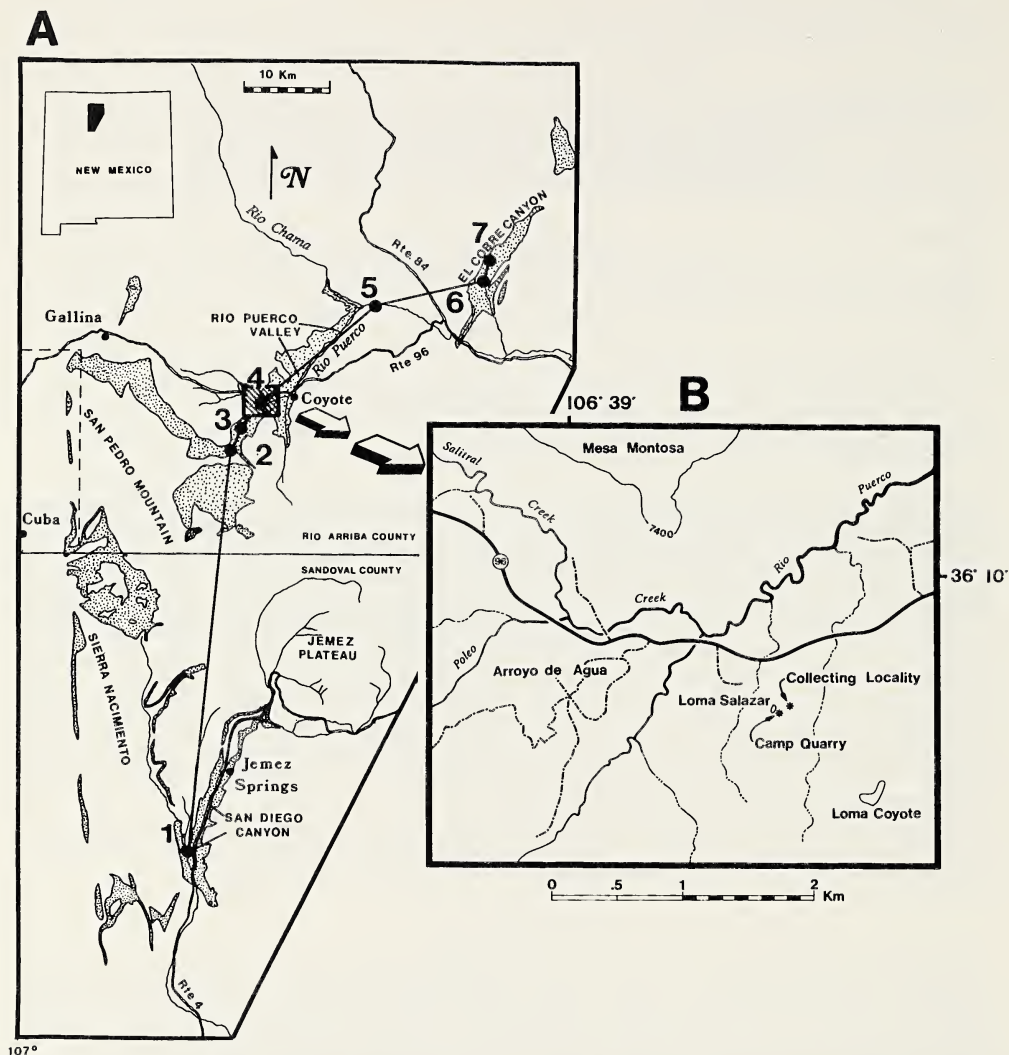


Fig. 1.—A, Locality map showing distribution of outcrops (stippled) of Permo-Pennsylvanian Cutler Formation (here including the Abo Formation of San Diego Canyon) of north-central New Mexico, and location of stratigraphic sections (numbers) shown in Figure 2. B, Detailed map of cross-hatched area of A showing locality from which the *Stegotretus agyrus* specimens described here were collected. Mesa Montosa and Loma Coyote are defined by 7400 and 7700 ft contour lines, respectively.

The long period of exploration before the discovery of the first unquestionable representatives of the Microsauria in the fossil-rich Permo-Pennsylvanian redbed deposits of north-central New Mexico is perhaps more surprising than their ultimate discovery. The Permo-Pennsylvanian of this region has received more attention from vertebrate paleontologists than all the other terrestrial beds of this age in New Mexico. This greater interest appears to have been well justified. In quantity, quality, and variety the Permo-Pennsylvanian vertebrate fossils discovered in the north-central region far surpass those from the rest of the state combined, and if the relatively small total area of exposures is taken into account,

may even rival those of the classic Lower Permian collecting beds of Texas and Oklahoma. The Permo-Pennsylvanian vertebrate faunas of New Mexico are in general similar to those of Texas and Oklahoma which, however, include a wide variety of microsaurs. In addition, Lower Pennsylvanian to Lower Permian microsaurs are known from Kansas, Colorado, and the central European and Great Britain coal measures (Carroll and Gaskill, 1978). The eventual discovery of microsaurs in New Mexico could have been anticipated.

ABBREVIATIONS

The abbreviations CM and UCPM are used to refer to the collections of The Carnegie Museum of Natural History and Museum of Paleontology, University of California, Berkeley, respectively.

Key to abbreviations used in figures: **a**, angular; **ad fo**, adductor fossa; **art**, articular; **at**, atlas; **bo**, basioccipital; **c**, coronoid; **cl**, clavicle; **ct**, coronoid tusk; **d**, dentary; **dp**, dermal plates; **eo**, exoccipital; **f**, frontal; **f cor**, coracoid foramen; **gl**, glenoid; **h**, humerus; **icl**, interclavicle; **imf**, inframeckelian fossa; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **pal**, palatine; **pf**, postfrontal; **pfr**, prefrontal; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **pra**, prearticular; **ps**, parasphenoid; **psp**, postsphenial; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, radius; **sa**, surangular; **sc**, scapulocoracoid; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **t**, tabular; **tric cor**, process for coracoid head of triceps; **u**, ulna; **v**, vomer; **x**, jugular foramen.

STRATIGRAPHY AND SEDIMENTOLOGY

The Cutler Formation occurs throughout north-central New Mexico as a thick, southwestward-thinning, subarkosic clastic wedge (Fig. 2). Although the unit is approximately 400 m thick in the Arroyo del Agua (= Arroyo de Agua of local parlance, see Langston, 1953) area of the Rio Puerco valley, only the uppermost 210 m of the formation is exposed there. Here the Cutler Formation redbeds consist of fine to granulitic, purple, red-brown, and grey feldspathic quartz arenites that are rich in altered biotite, locally conglomeratic, and interbedded with red-brown to variegated mudstones, siltstones, shales, and argillaceous limestones.

Eberth (1987) demonstrated that portions of three megasequences are present in the exposures of the Cutler Formation in three separate erosional valleys in north-central New Mexico that include not only the Rio Puerco valley, but also El Cobre Canyon and San Diego Canyon. By utilizing a combination of litho-, tectono-, and biostratigraphic data the megasequence portions were fitted together to produce the stratigraphic model shown in Figure 2. Cutler Formation deposition took place across the Pennsylvanian-Permian boundary (Smith et al., 1961; Fracasso, 1980; Eberth, 1987), but there is no discrete feature in the Cutler rock package that marks the boundary. Preexisting and new biostratigraphic data were used by Eberth (1987) in attempts to determine the age of portions of the clastic package (Fig. 2). It was concluded that, whereas the exposures in the Rio Puerco valley (including the Arroyo del Agua area) were largely of Wolfcampian age, basal exposures could conceivably be Virgilian in age. The specimens described here were collected from the base of the Cutler Formation exposures in the Arroyo del Agua area and, until more conclusive biostratigraphic data are available, are best referred to as Permo-Pennsylvanian in age.

The sedimentology of the Cutler Formation in north-central New Mexico has been described in detail by Eberth (1987), and the following information is obtained largely from that study. The sediments of the Cutler Formation are derived from the ancient Uncompahgre highland that extended from Colorado into New Mexico during Permo-Pennsylvanian time. The erosion of this largely granitic, crystalline basement complex resulted in the deposition of prograding, ephemeral

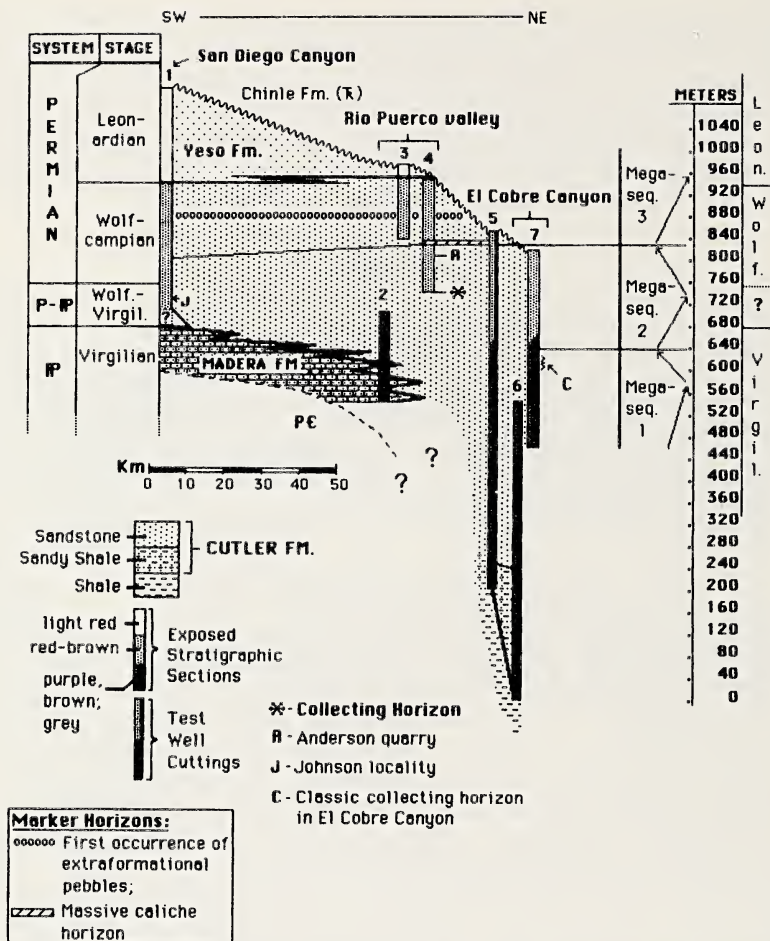


Fig. 2.—Stratigraphic model illustrating relationships of Permo-Pennsylvanian deposits of north-central New Mexico. Section localities are indicated in Figure 1A. Sections 1, 2, 3, 4, and 7 are composites indicating maximum thicknesses of exposures. Sections 5 and 6 are based on test-well cuttings (for details see Eberth, 1987). Vertical scale is not attached to any datum and shows only relative thicknesses of sections. The stratigraphic horizon from which the *Stegotretus agyrus* specimens described here were collected is indicated by the asterisk in section 4. The stratigraphic horizons of well-known fossil localities are indicated by letters (for detailed information see Langston, 1953; Fracasso, 1980; Eberth, 1987).

fluvial systems that drained a narrow coastal plain extending between the highlands to the north and a shallow regressive epeiric sea to the south. Low-sinuosity channels possessing a coarse-grained bedload dominated the floodplain, and anastomosed reaches were present locally. Ubiquitous, well-developed pedogenic carbonate profiles indicate that semi-arid climatic conditions prevailed during deposition of the Cutler Formation sediments. The basal Cutler Formation exposures in the Arroyo del Agua area exhibit numerous lithofacies, including three distinctive and key types (Fig. 3): 1) single- to multistoried sandstone ribbons; 2) locally occurring, fining-upward, U-shaped mixed-fill units; and 3) thick, laterally extensive, caliche-rich mudstones and siltstones. These three facies are interpreted as (1) vertically aggrading, low-sinuosity, anastomosed river channels, (2) sea-

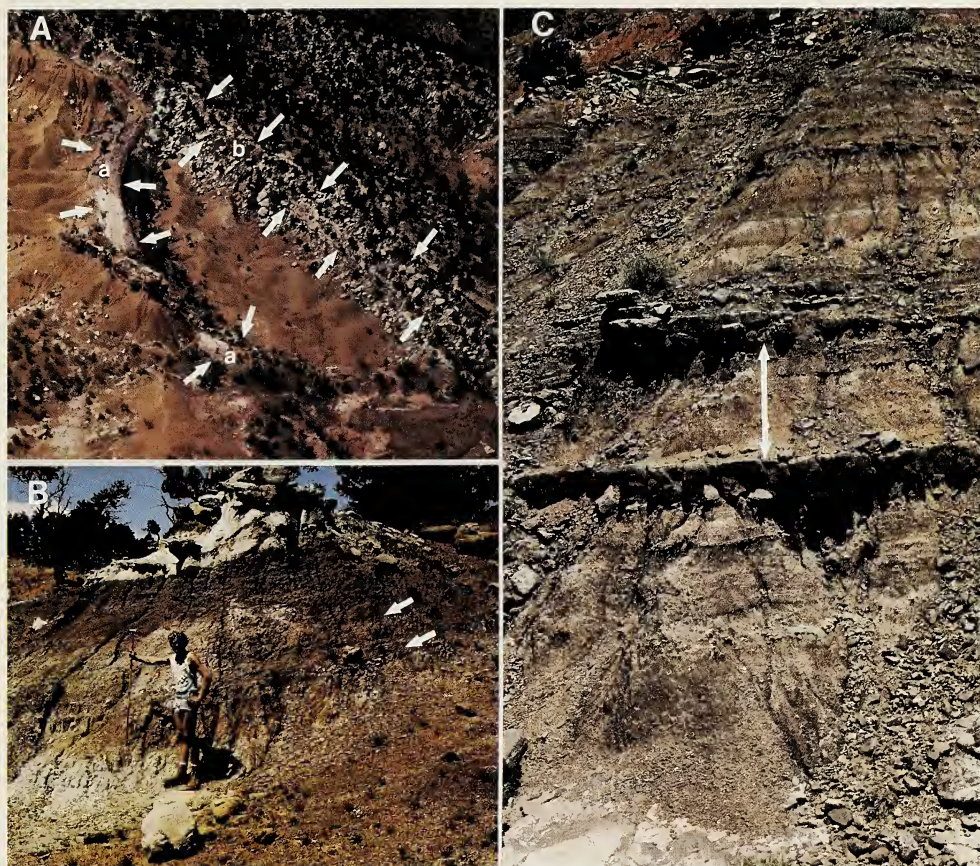


Fig. 3.—Key lithofacies from the Arroyo del Agua area of the Rio Puerco valley. A, Southward aerial view photograph of two sandstone ribbons indicated by arrows. Ribbon “a” is approximately 15 m wide and curves over a distance of 150 m toward the lower right. Approximate position of ribbon “a” with respect to fossil localities is shown by stippled area in Figure 4. Ribbon “b” is poorly defined owing to erosion and surface cover. B, U-shaped mixed-fill deposit (Vanderhoof quarry). Coarse sediments occur as grey/white reduced siltstones, sandstones, and gravels near base, and fine sediments occur as dark, oxidized mudstones and siltstones near top. Arrows define concentrically dipping bedding planes. C, Thick sequence of mudstones, siltstones, and caliches, and two thin sandstone sheets. Distance between sandstone sheets, indicated by double-headed arrow, is approximately 1.5 m. Subtle horizontal stratification defines stacked, ancient soil horizons.

sonally active (ephemeral) crevasse channels among the anastomosed channels that acted as small ponds for parts of the year, and (3) laterally extensive floodplains adjacent to anastomosed and other channel complexes that were dry for much of the year.

With one exception the microsaurs specimens described here were collected from partial to complete caliche nodules and calcite-rich siltstone pebbles littering a 4 m² surface of a small knoll northeast of the well-known Camp quarry (see Langston, 1953, for description of quarry) (Fig. 1). Caliches generally form in semi-arid to arid conditions where calcium is concentrated in the vadose zone of an exposed floodplain during seasonally alternating wet and dry periods. Trenching at this locality revealed more caliche nodules but no additional specimens, indicating that the fossiliferous bed had been long ago washed away and that the

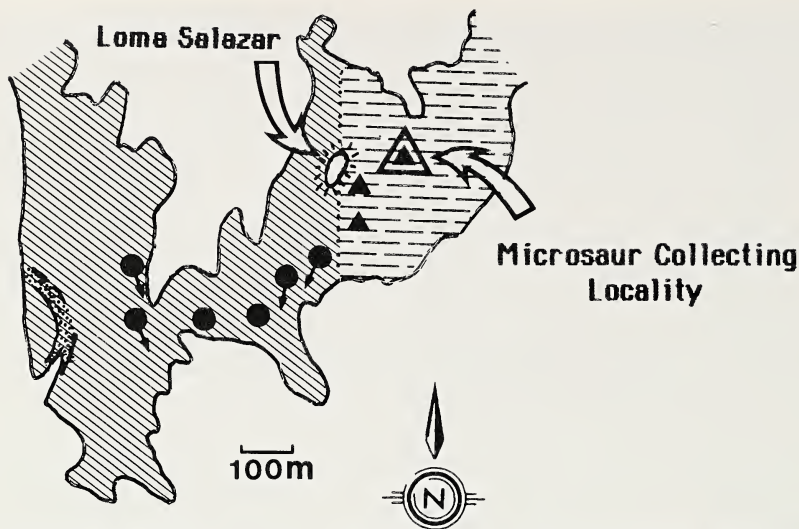


Fig. 4.—Geographic distribution of two stratigraphically equivalent lithofacies assemblages in the collecting area (see Fig. 1 for general location). Shaded areas represent the stratigraphic interval between 6800 and 6880 ft contour lines of U.S.G.S. Arroyo del Agua 7.5 minute quadrangle. Distribution of assemblage 1, comprising sandstone ribbons (Fig. 3A) and a large number of U-shaped mixed-fill units (Fig. 3B), and assemblage 2, comprising thin (< 50 cm thick) sandstone sheets and numerous, thick laterally extensive, caliche-rich mudstone and siltstone beds (Fig. 3C), are indicated by cross-hatching and dashed lines, respectively. Black circles indicate the locations of some U-shaped mixed-fill units, many of which are famous vertebrate collecting sites, black arrows indicate paleoflow directions, stippled area to west indicates approximate position of locally prominent sandstone ribbon shown in Figure 3A, and black triangles indicate some vertebrate collecting sites in assemblage 2 area.

nodules, pebbles, and associated fossils are a surface lag. The matrix associated with the specimens is a calcite-rich, redbrown (3/42.5YR–4/41OR) sandy, fine siltstone. There is no evidence of ribbon sandstones or U-shaped mixed-fill units at the collecting locality. The association of caliche with the microsaur specimens, the presence of a massive siltstone matrix, and the absence of ribbon sandstones and U-shaped mixed-fill facies at the collecting site all suggest that the specimens were originally preserved in an overbank floodplain setting.

Within the general collecting area described here (1 km²) two stratigraphically equivalent, but paleogeographically discrete, lithofacies assemblages can be identified (Fig. 4), both comprising stratigraphic intervals of approximately 25 m. One of the lithofacies assemblages occurs west of the collecting locality and comprises sandstone ribbons (Fig. 3A) and a large number of U-shaped mixed-fill units (Fig. 3B). Thick caliche-rich mudstone and siltstone deposits are also present. Vertebrate fossils are particularly abundant in the lower horizons of many of the mixed-fill units, and many of the classic bonebeds and quarries described by Langston (1953) (e.g., VanderHoof quarry, Welles quarry, Quarry Butte) occur in mixed-fill units. This lithofacies assemblage is interpreted as the partial remains of a locally anastomosed river system comprising southward flowing, laterally stable, vertically aggrading, low sinuosity channels and a network of ephemeral crevasse channels that were temporary sites of standing water. The second lithofacies assemblage occupies the area immediately surrounding the collecting locality (within a 150 m radius). It consists of thin (< 50 cm thick) sandstone sheets and numerous thick, laterally extensive, caliche-rich mudstone and siltstone beds (Fig. 3C) which have been interpreted as crevasse splay and overbank suspension deposits, re-

spectively. It is the site of numerous isolated vertebrate localities and is also the site of the Camp quarry which has produced a unique fossil assemblage, including one specimen of the microsauro described here.

We hypothesize that both lithofacies assemblages represent, in a general sense, time equivalent, laterally adjacent environments that aggraded vertically and were laterally stable for considerable time. Although litho- or chronostratigraphic correlation of the individual facies between the two areas is not possible, the modest vertical thickness (25 m) of these laterally discrete facies assemblages attests to a long period during which the anastomosed river channels with their interchannel wetlands and adjacent floodplain occupied this general area. Within the context of this simple model, the microsauro locality occupied a position on a proximal portion of the floodplain some 150 m west of a southward flowing, anastomosed channel complex.

SYSTEMATIC PALEONTOLOGY

Class Amphibia
Order Microsauria
Suborder Tuditanomorpha
Family Pantylidae

Revised definition. — Small to moderate-sized microsaurs characterized by the following shared-derived features: 1) sutural pattern of lacrimal-jugal contact beneath orbit appears as overlapping processes; 2) prominent dorsal expansion of maxilla; 3) conspicuous ventral expansion of the postorbital cheek region formed mainly by the jugal which greatly overlaps laterally the posterior end of the maxilla and conceals, or partially conceals, the posterior end of the upper tooth row; 4) no ectopterygoid; 5) internal naris greatly enlarged to accommodate two anterior dentary teeth; 6) second dentary tooth much larger than others of dentary series; 7) extremely large, tusk-like tooth on the coronoid of lower jaw; 8) scapulocoracoid has an abrupt right angle union between the scapular and coracoid portions, a long, narrow glenoid whose anterior and posterior ends are at the same level and that is positioned well posterior of scapula, and a prominent, triangular process near the posterior border of the glenoid for origin of coracoid head of triceps.

Stegotretus, new genus

Type species. — *Stegotretus agyrus*, new species.

Etymology. — From the Greek *stegos*, roof, and *tretos*, perforated, referring to the large, circular fenestra of the palatine bone.

Diagnosis. — Can be distinguished from all other microsaurs by the autapomorphies of only two premaxillary teeth and palatine with a large, circular fenestra. Derived characters separating *Stegotretus agyrus* from its nearest relative, *Pantylus*, include contact between maxilla and quadratojugal, and absence of entepicondylar foramen of humerus.

Stegotretus agyrus, new species

Etymology. — Greek, *agyrus*, meaning gathering or crowd, referring to the occurrence of all but one of the specimens in a very small area.

Holotype. — CM 38023 consists of an essentially complete skull with tightly closed jaws.

Paratypes. — CM 27559, partial skull; CM 27574, skull; CM 28581, partial skull with long series of vertebrae and articulated pelvic girdle, femora, and right tibia

with part of pes closely associated; CM 28582, skull; CM 28583, partial articulated skeleton that includes skull, first five vertebrae, scapulocoracoids, interclavicle, clavicles, left humerus, and dermal plates associated with shoulder girdle; CM 28584, skull; CM 28585, several series of vertebrae with associated ribs; CM 33998, small portion of skull showing mainly anterior part of palate; CM 33999, small portion of skull showing mainly anterior portion of palate; CM 34100, skull; CM 34901, skull; CM 34902, series of five vertebrae and right scapulocoracoid and articulated distal end of humerus with small patch of dermal plates; CM 34903, two series of four and seven vertebrae; CM 41715, skull; CM 41716, skull; CM 41717, skull; CM 41718, small portion of skull showing mainly posterior part of palate; CM 41719, portion of skull showing mainly posterior half of left side of dermal roof; CM 41720, skull; CM 41721, greater part of skeleton that includes skull, long series of trunk vertebrae, articulated right scapulocoracoid, humerus, radius, ulna, and fragments of carpus, patches of dermal plates associated with shoulder girdle; CM 41722, partial skull showing mainly the roof; CM 41723, skull articulated with first seven vertebrae; CM 41723, skull. Most skulls have tightly closed lower jaws.

Horizon and locality.—All specimens are from the lowermost level of the exposed section of the Cutler Formation on the Rio Puerco drainage, Rio Arriba County, north-central New Mexico. This level of the section is best considered Permo-Pennsylvanian in age (see STRATIGRAPHY AND SEDIMENTOLOGY section above). All but one specimen (CM 41717) were collected from the surface of a small, weathered knoll about 82.5 m N 58° E of the Camp quarry (Fig. 1B) (see Langston, 1953, for description of locality). CM 41717 was collected on the surface immediately adjacent to Camp quarry. Both localities are located in SW1/4NE1/4NE1/4 sec. 8, T 22 N, R 3 E, about 1.1 km southeast of Arroyo del Agua.

Diagnosis.—Only known species.

Description

Skull.—Although the specimens of *Stegotretus agyrus* are represented by numerous complete or partial skulls, many imperfections of their preservation have made interpretation of the cranial anatomy difficult. Most of the skulls were preserved in caliche nodules and many of these were exposed, for the most part, by fracturing away the surrounding matrix in small blocks or chips. Unfortunately, considerable amounts of the external dermal bones spalled off in this process, greatly distorting the course of the external contacts of overlapping sutures. In a couple of instances it was possible to reassemble some of the surrounding blocks of matrix into a partial counterpart block. The adhering bone of the counterpart block was removed so as to create a natural mold from which a silastic rubber cast was made. The recrystallization of calcite within the dermal bones has also caused some exfoliation of bone. In a few instances the skulls have been exposed by weathering, but this has also resulted in great erosional loss of the dermal bone. The tracing of sutures in most of the skulls is also made difficult, if not impossible, by extensive fracturing of the bones. All but two of the skulls (holotype CM 38023, and 28582) appear to have suffered moderate to severe distortion from dorso-ventral crushing. The only very noticeable distortion to the holotype has been the crushing of the right, postorbital cheek region (Fig. 5A). This specimen is the basis for much of the reconstruction of the skull and lower jaw of Figure 10. Cranial measurements for all the skulls are given in Tables 1 and 2. To facilitate comparisons with other microsauro species we have, for the most part, employed the same series of measurements used by Carroll and Gaskill (1978) in their review

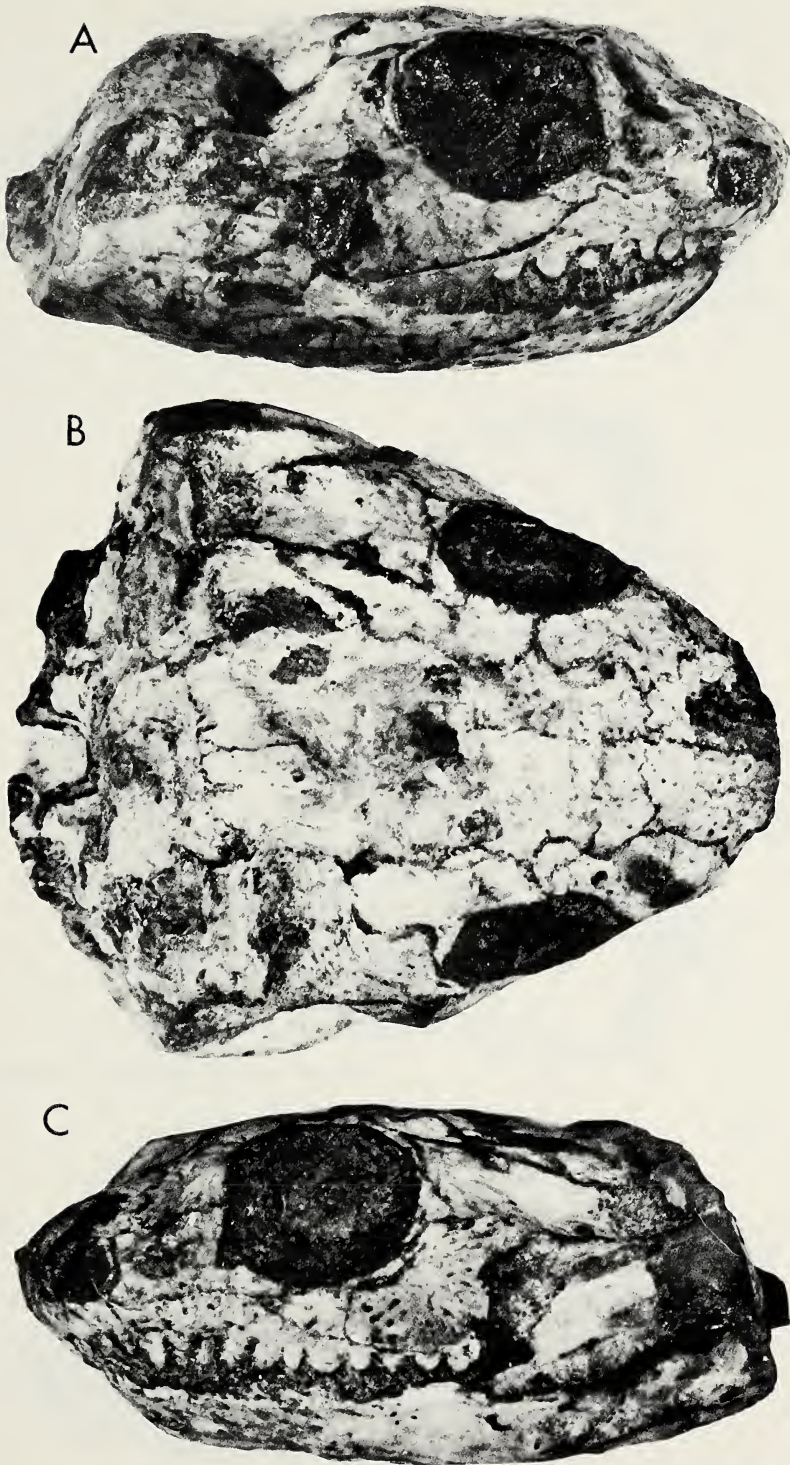


Fig. 5.—*Stegotretus agyrus*, holotype, CM 38023. Skull in A, right lateral; B, dorsal; and C, left lateral views.

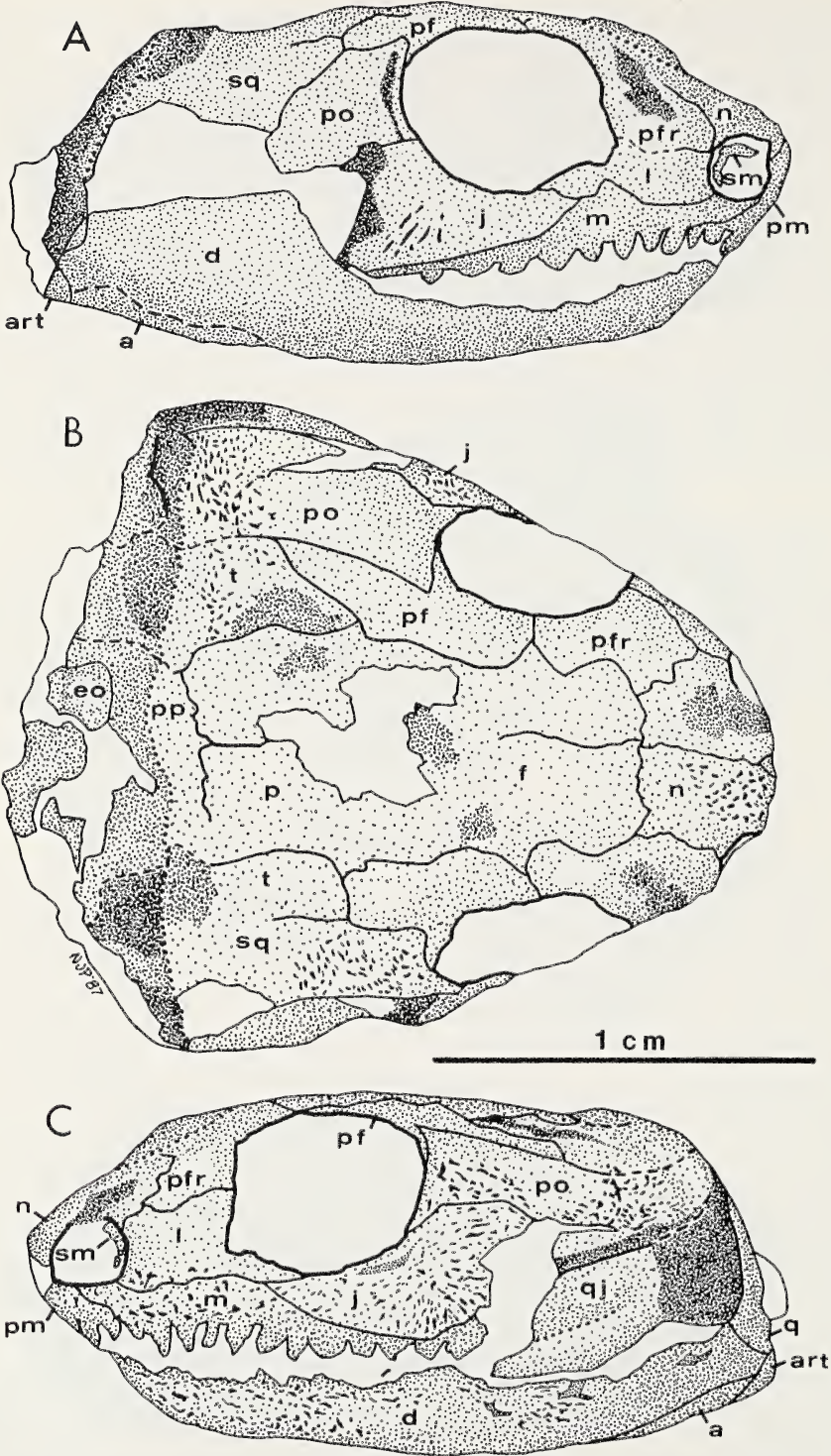


Fig. 6.—*Stegotretus agyrus*, holotype, illustrations of CM 38023 as seen in Figure 5.

Table 1.—Skull measurements (in mm) of *Stegotretus agyrus* specimens. Abbreviations: AL, antorbital length; HC, height of cheek; IO, interorbital width; LM, length of skull margin to quadrate; LO, length of orbit; LS, length of skull; LT, length of tooth row; ON, orbit to naris distance; OQ, distance of occiput behind jaw suspension; PL, postorbital length; WS, width of skull (most measurements as in Carroll and Gaskill, 1978). Oblique slash separates measurements for left and right sides. * indicates distortion of region from which measurement was taken and ** indicates holotype.

Specimen	LS	WS	HC	LM	LT	LO	AL	PL	OQ	ON	IO
CM 28581			8.3/			4.5/4.3		/8.3			6.2
CM 28582	20.0	21.7	/7.5*	/20.5*	/13.0	/5.3	9.2/7.2	/10.0		/3.7	7.8*
CM 28583	20.4	22.1*	/6.3*	20.0/20.7	/11.7	5.0/5.0	6.6/6.1	10.1/9.8	2.0*	3.6/3.3	6.8*
CM 34901	19.2*	18.0*	7.0/3.7*	17.7/	11.3/	4.9/4.9			2.1*	2.7/2.9	7.0
CM 38023**	18.5	16.9	5.5/	17.3/	11.1/11.8	4.5/4.4	5.8/5.5	7.7/8.1	1.0*	3.0/3.0	6.9
CM 41715						4.1/		7.8/			6.0
CM 41716	14.8	12.0*	4.1*/	13.4/12.8	8.2/8.1	3.2/3.2	4.5/4.7	7.8/6.2	1.0*	2.5/2.5	3.6
CM 41717	13.7	13.3*	/3.0*	13.6/12.7	8.8/8.0	3.6/3.6	4.8/4.8	5.8/4.7		/2.5	5.3
CM 41719						5.5/		8.4/			
CM 41720	21.6	20.7*	5.0*/	18.9/19.2	11.9/12.5	4.2/4.5	6.8/6.9	10.4/10.0	1.7*	/3.5	9.4
CM 41721	16.4	14.7*	4.0/3.6*	14.3/15.7	11.0/	4.2/3.9	5.0/5.3	7.6/6.7	1.7*	2.5/	5.4
CM 41722			5.5/			5.4/					8.9
CM 41724						6.3/					9.3

Table 2.—*Skull proportions of Stegotretus agyrus based on measurements of Table 1. Abbreviations: Ave Und, average value for undistorted specimens; N, sample size (includes both sides of skull); N Und, number of undistorted specimens; SD, standard deviation. See Table 1 for other abbreviations. Oblique slash separates measurements for left and right sides. * indicates distortion of region from which measurement was taken and ** indicates holotype.*

	$\frac{WS}{LS}$	$\frac{HC}{LS}$	$\frac{AL}{LS}$	$\frac{LO}{LS}$	$\frac{PL}{LS}$
Specimen					
CM 28582	1.085	/0.38*	0.460/0.360	/0.265	/0.50
CM 28583	1.083*	/0.31*	0.324/0.299	0.245/0.245	0.495/0.48
CM 34901	0.938*	0.37*/0.19*		0.26*/0.26*	
CM 38023**	0.914	0.297/	0.314/0.297	0.243/0.238	0.416/0.438
CM 41716	0.81*	0.28*/	0.304/0.318	0.216/0.216	0.527/0.419
CM 41717	0.971*	/0.22*	0.350/0.350	0.263/0.263	0.423/0.343
CM 41720	0.958*	0.23*/	0.315/0.319	0.194/0.208	0.481/0.463
CM 41721	0.896*	0.244/0.22*	0.305/0.323	0.256/0.238	0.427/0.409
N	8	10	14	15	13
Average	0.963	0.273	0.331	0.241	0.448
SD	0.098	0.064	0.042	0.023	0.049
Range	0.85–1.085	0.190–0.375	0.297–0.460	0.194–0.265	0.343–0.527
N Und	2	2		13	
Ave Und	1.000	0.271		0.238	

of the order, and their paper should be consulted for the exact orientations of the measurements.

Despite varying degrees of dorsoventral crushing, the New Mexico microsauroid skulls were obviously proportionally very wide. Skull width to length ratios range from about 0.85 to 1.09, and it is suspected that the actual value was close to the average of 0.96. The skull table is nearly flat and meets the nearly vertical postorbital cheek region in a rather abrupt angle. In the reconstruction of Figure 10 the skull height at the level of the cheek is restored at the upper level of the range of values recorded for all the specimens, which is from about 19.0 to 37.5% of the skull length. The depth of the posterior portion of the skull decreases only slightly anteriorly to about the level of the anterior border of the orbit. At this point there is in lateral view a sharp downward slope to the tip of the bluntly rounded snout, which overhangs moderately the tooth row. The large, subcircular orbits face nearly laterally. The length of the orbits ranges from 19 to 26% of the skull length, but there is no indication that this range of values reflects an allometric growth relationship. The orbits lie extremely far forward, with the antorbital length to skull length ratio ranging from 0.30 to 0.46. Judging from the measurements of Table 2, the upper end of this range is obviously erroneous, and this proportion was probably near the average value of 0.33, which is approximately that used in the reconstruction of Figure 10. The narial opening is large and subcircular. Coincident with the short antorbital length of the skull is the extremely short distance between the orbit and naris, which ranges from 14.0 to 18.5% of the skull length. The occiput slopes slightly anterodorsally and has a nearly straight margin with the skull table. The occipital condyle is positioned posterior to the level of the jaw articulation at a distance that ranges from about 5.5 to 11.0% of the skull length; the true value is probably near the average, 8.5%. There is a noticeable downward expansion of the ventral margin of the postorbital region of the skull formed mainly by the jugal. There is no evidence of a palpebral cup or sclerossicles. Most of the ornamentation of the dermal skull bones has been lost. In addition to a sculpturing pattern of minute pitting seen on some of the dermal skull bones of the holotype (CM 38023) and CM 41717, the left jugal of the holotype exhibits a radiating pattern of short grooves.

The dorsal process of the premaxilla is very short and tapers to the midline. The maxillary process is overlapped laterally by the maxilla, and the premaxilla forms only the anterior border of the external naris. The premaxilla possesses two stout teeth, the first being typically about 25 to 50% larger than the second and equal in size to the largest of the maxillary series. A narrow, strip-like septomaxilla borders the posterior half of the naris, excluding the lacrimal and portions of the nasal and maxilla from the external naris. There appears to be an abrupt expansion of the dorsal end of the septomaxilla.

Table 2.—Continued.

$\frac{LM}{LS}$	$\frac{LT}{LM}$	$\frac{OO}{LS}$	$\frac{ON}{LS}$	$\frac{IO}{LS}$
/1.025	/0.634		/0.185	0.39
0.980/1.01	/0.565	0.098	0.176/0.162	0.333*
0.92*/	0.638/	0.109*	0.140*/0.150*	0.365*
0.935/	0.642/	0.054	0.162/0.162	0.373
0.905/0.865	0.612/0.633	0.068	0.169/0.169	0.243
0.993/0.927	0.647/0.630		/0.182	0.387
0.875/0.889	0.630/0.651	0.079	/0.162	0.435
0.872/0.957	0.769/	0.104	0.152/	0.329
13	11	6	12	8
0.935	0.641	0.085	0.164	0.357
0.054	0.048	0.022	0.013	0.057
0.865/1.03	0.565–0.769	0.054–0.109	0.140–0.185	0.243–0.435
12		5	10	6
0.936		0.081	0.168	0.360

The nasals (Fig. 9A) are relatively short and have a greatest anteroposterior length of only slightly over half those of the subequal frontals and parietals. A substantial contact between the prefrontal and postfrontal excludes the frontal from entering the orbital margin. The rectangular parietals bound the pineal foramen at about their midlength. The postparietals appear to have a more extensive exposure on the occiput than on the skull table.

The prefrontals closely approach but do not enter the narial border. The postfrontal is noticeably shorter in posterior extent than the postorbital; about one third the length of the postorbital extends posteriorly beyond the postfrontal. The lacrimal tapers only slightly anteriorly and has a broad contact with the septomaxilla. Posteriorly the lacrimal possesses a noticeable ascending orbital process on the anterior orbital margin, whereas along the suborbital margin it narrows to a thin, wedge-like process that extends above a similar wedge-like anterior process of the jugal. The sutural relationship between the lacrimal and jugal is well exemplified on both sides of the holotype due to very little erosion or distortion. The maxilla is of normal length, extending posteriorly well beyond the orbit. However, approximately the posterior third of the maxilla and its contact with the quadratojugal are concealed from lateral view by the ventrally expanded jugal, which extends for a considerable length along the ventral margin of the skull. The maxilla exhibits a prominent dorsal expansion at the level of the anterior margin of the orbit. The maxilla possesses 11 to 12 stout, conical teeth. Their serial size relationships, however, seem to vary in the few specimens in which the series is complete enough to describe. The maxillary dentition of the holotype is depicted in the reconstruction of Figure 10. The first six or seven teeth are subequal in size, followed by one or two that are noticeably larger but not enough so as to be described as caniniform, and the remaining three to four teeth are subequal in size and smaller than the others of the series. In CM 34901 and 41720 there is a more or less gradual decrease in size posteriorly from the second and largest tooth of the maxillary series, with the first tooth approximating the size of the third through sixth teeth. The percentage of the skull margin occupied by the combined premaxillary and maxillary marginal tooth rows ranges from about 57 to 77%; the distribution of values, however, suggests that the correct value was most likely close to the 64% of the holotype.

The quadratojugal is limited in lateral view to a dorsoventrally narrow, rectangular exposure that extends along the ventral margin of the cheek. The extent of the quadratojugal in the cheek region is much greater than that indicated by its lateral exposure. It not only underlaps the jugal for a short distance, but has an extensive dorsal expansion that is overlapped by the squamosal. As on the left side of the holotype (Fig. 5C), in many of the specimens most or all of the squamosal has been lost, revealing the great dorsal expanse of the quadratojugal. There is evidence that at least a narrow margin of the ventral border of the quadratojugal wrapped around the posterior edge of the cheek medially

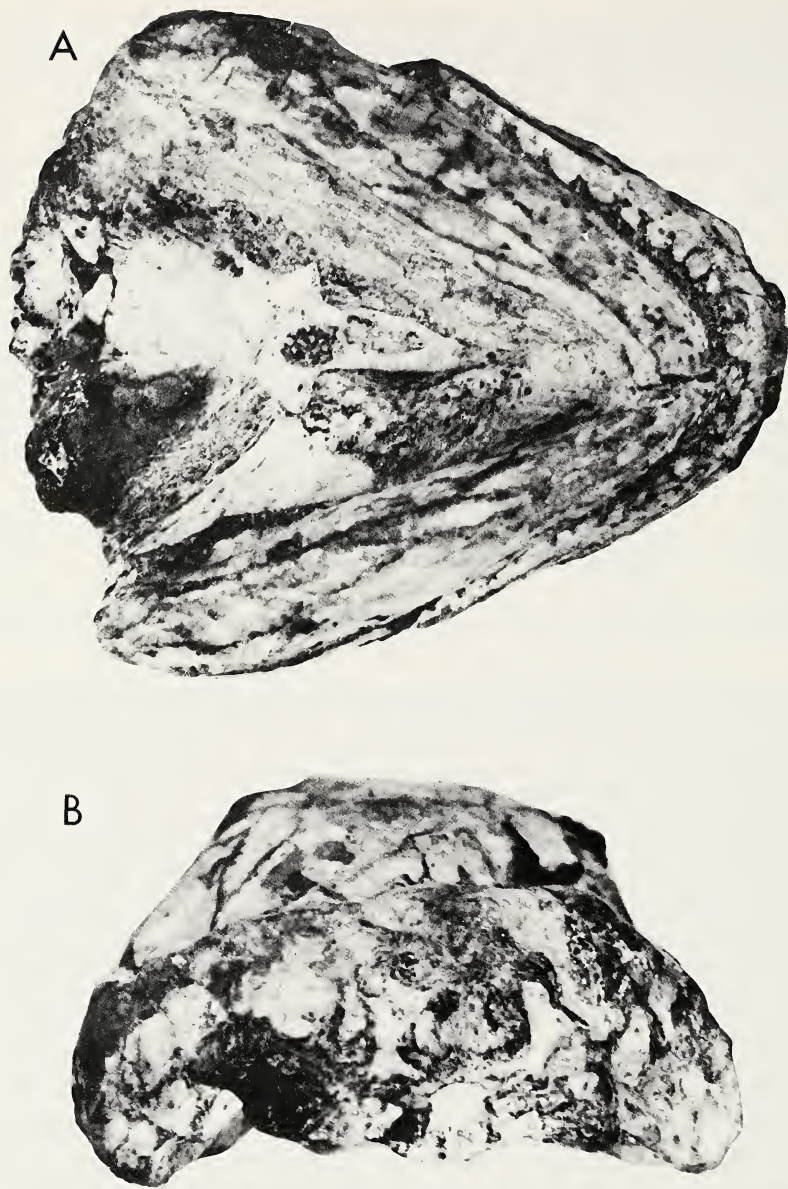


Fig. 7.—*Stegotretus agyrus*, holotype, CM 38023. Skull in A, ventral; and B, occipital views.

and was interposed between the anterior quadrate and the posterior occipital flange of the squamosal. In the holotype (Fig. 7B, 8B) the occipital flange of the left squamosal is missing, revealing that it covered a vertically ascending process of the quadrate of approximately the same height and width. A small, ventrally directed, spike-like orbital process of the postfrontal encroaches on the orbital contribution of the postorbital, and a similar process of the postorbital invades the orbital margin of the jugal. Like the postparietal, the tabular and squamosal have large occipital flanges.

Each vomer (Fig. 9, 10) is greatly reduced to a narrow, tooth-bearing element that bounds medially the very large, kidney-shaped internal naris. The vomers are united medially for only about the anterior half of their length, being separated posteriorly by the pterygoids. At the anterior end of their union the vomers narrow to short, splint-like processes which are clasped between two very short processes

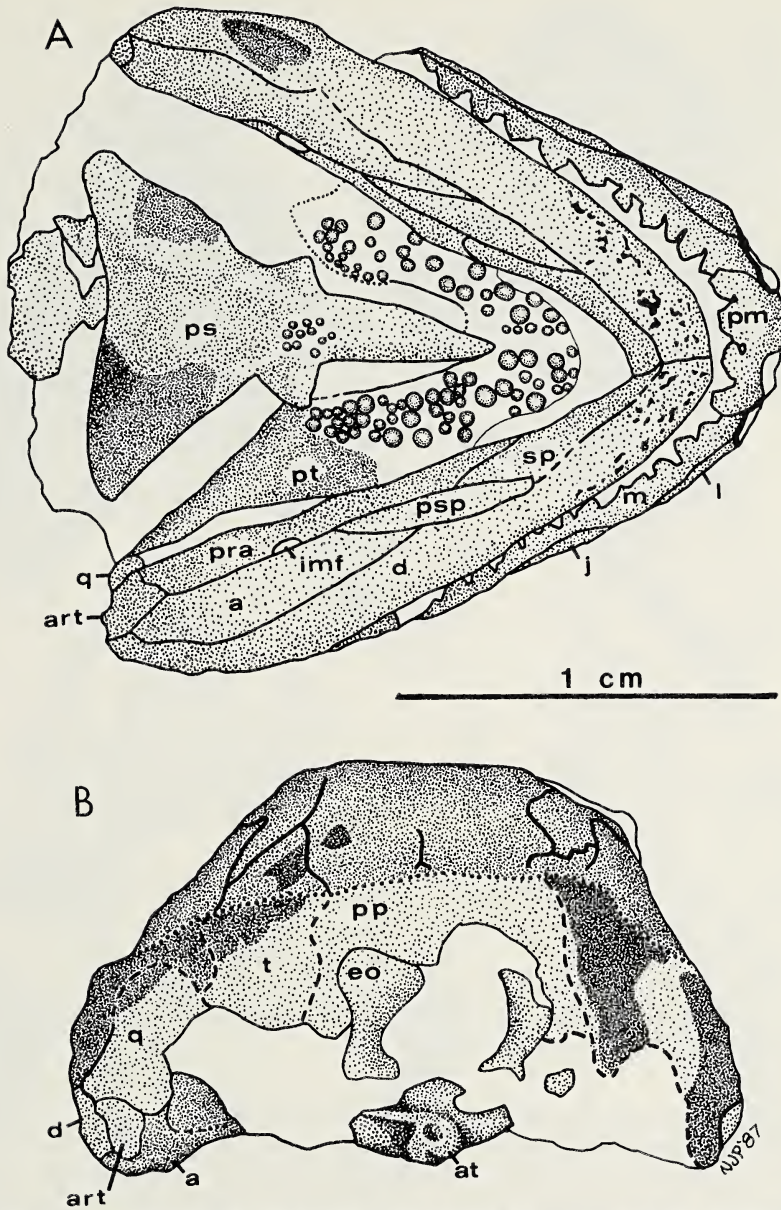


Fig. 8.—*Stegotretus agyrus*, holotype, illustrations of CM 38023 as seen in Figure 7.

from the posteromedially joined premaxillae. Posteriorly the vomer has a sharply angled suture with the palatine. The large, rectangular palatine dominates the palate. Its only free border is that forming the posterior margin of the internal naris. The entire surface is covered by very stout and rather densely packed teeth which exhibit a slight tendency to increase in size toward the lateral margin. At the posterior end of the lateral margin of the palatine there occurs one or more strikingly larger teeth approaching the size of the largest marginal teeth of the maxilla. There is no indication that the palatine teeth, nor those of the other tooth-bearing elements of the palate, are arranged in any discernable pattern. A striking feature of the palatine is a large circular fenestra located just posterolateral to its center. In at least two specimens (CM 34100, 41715; Fig. 9D) the tip of a large tusk-like coronoid

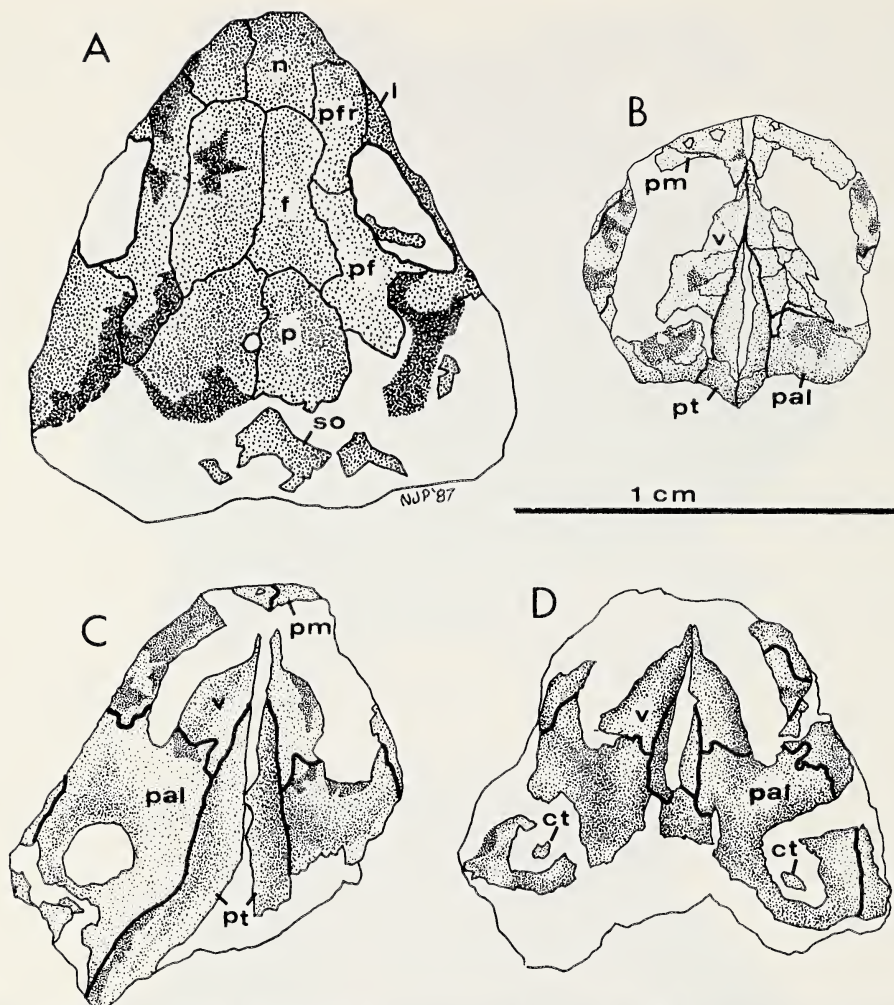


Fig. 9.—*Stegotretus agyrus*, paratypes. A, dorsal view of skull CM 41717. B–C, partial palates of CM 33999, 33998, and 41715, respectively.

tooth occupies the center of the openings (see below). The pterygoid is triradiate. A thin anterior ramus borders the palatine medially and a narrow interpterygoid vacuity laterally, then joins its mate in a median suture to wedge between the posterior halves of the vomers. The united portions of the anterior rami and the medial margins of the vomers are vaulted steeply dorsomedially, forming a groove-like, midline channel. A narrow, lateral or transverse ramus of the pterygoid borders the palatine posteriorly. For a short distance posterior to the anterior and lateral rami the pterygoid forms a broad, slightly concave central palate. Posterior to the level of the basal articulation the pterygoid narrows as the quadrate ramus twists dorsomedially to a nearly vertical plane. The quadrate ramus almost reaches the occiput, overlapping medially a short pterygoid process of the quadrate. With the possible exception of its narrow lateral ramus bordering the subtemporal fossa, the pterygoid is covered anteriorly from about the level of the basal articulation by small, densely-packed teeth. The pterygoid does not appear to have any recess or socket for the reception of the basiptyergoid process of the braincase. The process contacts the ventromedial margin of the pterygoid at a level just posterior of where it begins to turn laterally to form the quadrate ramus. The quadrate is narrowly visible in occipital view just below the occipital flanges of the squamosal and quadratojugal. A completely exposed articular surface is not available in any of the specimens, but it was obviously an anteroposteriorly narrow, convex surface. A very unusual feature of the palate is the absence of an ectopterygoid.

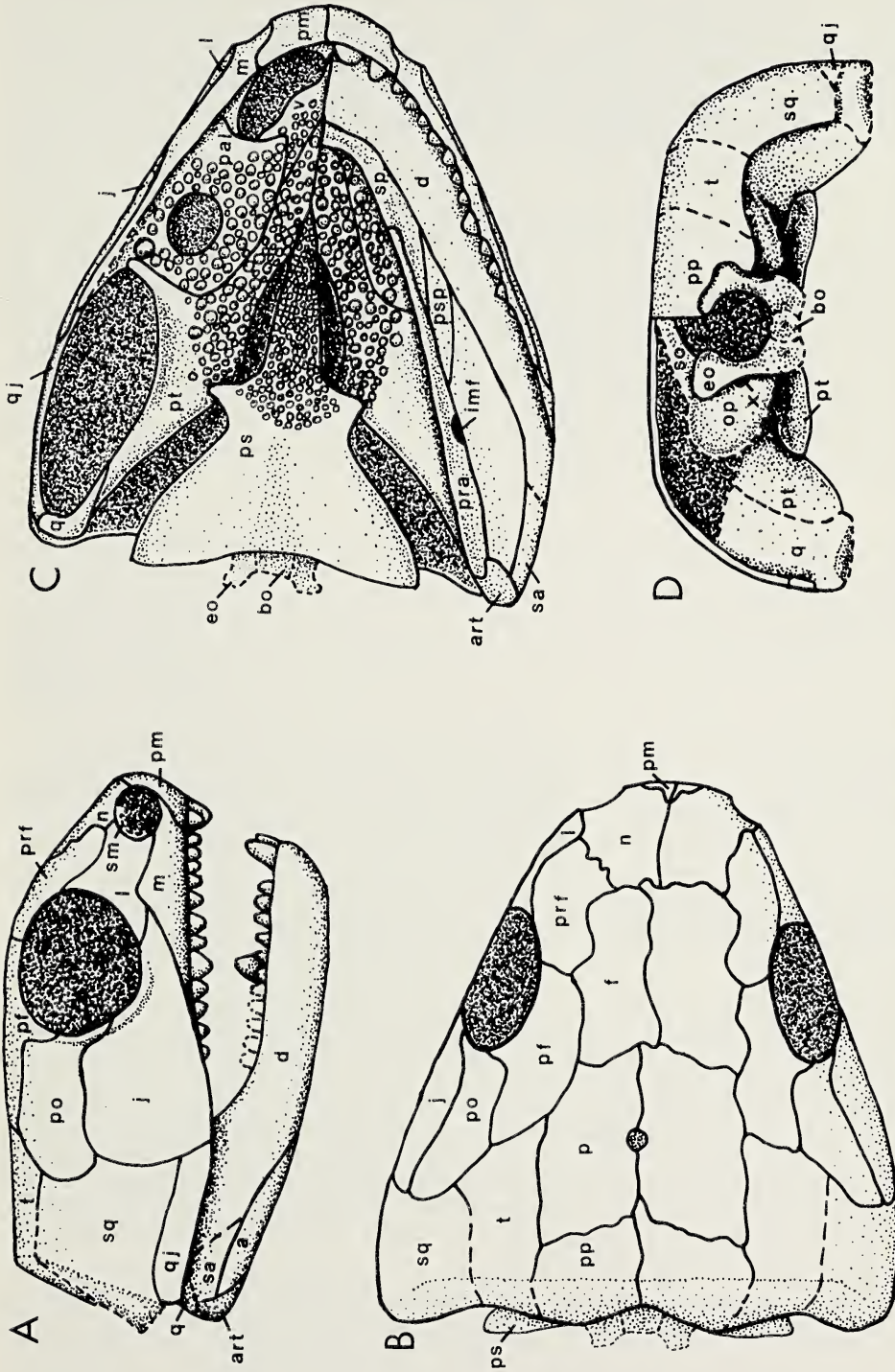


Fig. 10.—Reconstruction of skull of *Stegocephalus agyrus* in A, lateral; B, dorsal; C, ventral; and D, occipital views. Right ramus in C and both rami in D absent. Based mainly on holotype CM 38023.

Much of the reconstruction of the occiput and braincase is tentative owing to the generally poor preservation of the specimens. The large occipital lappets of the paired postparietals extend ventrally, completely covering the supraoccipital, bounding the dorsal margin of the foramen magnum, and overlap the upper end of the dorsal process of the exoccipitals. The ventral margin of the combined occipital lappets of the tabular and squamosal arches smoothly ventrolaterally to the jaw joint. Where the occipital lappets of the postparietals are lost (CM 28581, 28583, and 41717, Fig. 9A) the supraoccipital is seen as a narrow arch that expands gradually toward its respective bases as it spans between the dorsal processes of the exoccipitals and the dorsomedial margins of the otic capsules. The dorsal processes of the exoccipitals, which form the lateral margins of the foramen magnum, flare strongly dorsally. In none of the specimens is the base of the exoccipital well enough exposed to reveal a hypoglossal foramen. The structure of the occipital condyle, although only partly observable in a few specimens, is undoubtedly typical of microsaurs; together the basioccipital and exoccipitals form a broad, dorsoventrally narrow, strap-shaped articular recess. The part of the condyle formed by the basioccipital is deepened at the midline to receive the "odontoid" process of the atlas. The occipital condyle projects beyond the posterior margin of the parasphenoid. Partially preserved otic capsules are visible in CM 28583 and 41715, and though the right otic capsule of CM 28581 is essentially complete, it is exposed mainly in occipital view. A proötic-opisthotic division cannot be discerned in CM 28581, and it is likely that only the opisthotic portion of the otic capsule is visible in this aspect. The otic capsule is thin-walled and extends far laterally and slightly anteriorly from its tight union with the anterior margin of mainly the dorsal process of the exoccipital. A jugular foramen appears to be present at the midheight along this contact in CM 28581. The otic capsule is essentially disk-shaped with a slightly convex outer surface. No stapes was found in any of the specimens.

The well-developed parasphenoid almost completely covers the braincase ventrally. The cultriform process of the parasphenoid is broad, but it tapers to a median point at the posterior level of the conjoined pterygoids. Transverse breaks through the skull of CM 34100 at several levels near the anterior end of the cultriform process reveal a very tall, U-shaped sphenethmoid resting on the parasphenoid. The thin, ascending flanges of the sphenethmoid rise to join the frontals and parietals. The main body of the parasphenoid is an extremely broad, triangular plate that underlies most of the posterior portion of the braincase. Centrally it is slightly concave, whereas its lateral wings are strongly convex. The parasphenoid extends far posteriorly, with the tips of its lateral wings probably extending beyond the level of the occiput so as to be visible in dorsal view of the skull. The triangular basiptyergoid processes are directed laterally, and their articular surface faces dorsolaterally and slightly anteriorly. Very small, closely spaced teeth cover the parasphenoid from between the basiptyergoid processes to the tip of the cultriform process. There are no signs of foramina for the internal carotid arteries.

Of isolated lower jaws there are only fragmentary remains. The only essentially complete jaws are those articulated with the skulls of some specimens, but because they are tightly adducted to the skull a direct view of the articular, occlusal, and adductor fossa regions is unfortunately not possible. The lower jaw is best represented in the holotype (CM 38023; Fig. 5-8). The outer surface of the jaw is convex, whereas the inner is flat and vertical. In lateral view the ventral margin of the jaw is broadly convex. The dentary is the dominant element on the external surface of the jaw and forms most of the symphysis. The dentary-surangular suture cannot be discerned in any of the specimens, but the dentary probably formed most of the moderately developed coronoid process. The angular is narrowly exposed laterally along the ventral border of the jaw; it extends a little over half the length of the jaw from its posterior end as it wedges anteriorly beneath the dentary. The angular wraps around the ventral margin of the jaw to have a very narrow exposure along the ventral margin of the internal surface. The two splenials occupy a very narrow strip along the ventral margin of the external surface of the jaw, extending a little over half the jaw length back from the limited splenial symphysis. The anterior splenial continues onto the internal surface of the jaw, where it almost completely sheaths the anterior fourth of the internal surface. Its contact with the prearticular posteriorly is nearly vertical except for within a very short distance of the ventral jaw margin; here the suture turns abruptly posteriorly to intersect the postsplenial at about midlength along its ventromedial border. The postsplenial is narrowly diamond-shaped; it does not extend onto the internal surface of the jaw. A small inframeckelian foramen is located on the angular-prearticular suture a short distance behind the posteriormost extent of the postsplenial. The articular appears to be narrowly exposed at the posterior end of the jaw; there is no retroarticular process.

The dentary held 10 to 12 stout, conical marginal teeth. The second is clearly the dominant tooth of the series, being approximately twice the size of the first, whereas, in general, the first tooth is considerably larger than the third and is only slightly larger than the fourth; the rest of the series decreases gradually in size posteriorly from the fourth. The first and second teeth were undoubtedly received into an enlarged internal naris when the jaws were closed. The number of coronoids is not known. The coronoid(s) and its (their) dentition are visible in only a few specimens as a result of

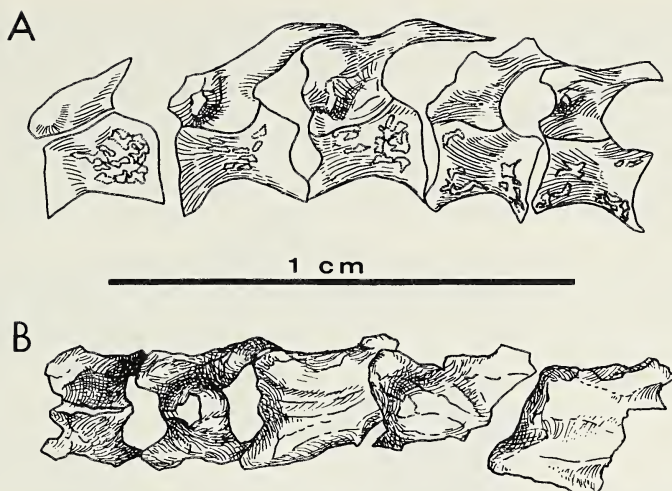


Fig. 11.—*Stegotretus agyrus*, paratype, CM 34903. A, lateral; and B, dorsal views of series of presacral vertebrae.

breaks in skulls with attached lower jaws, and very little can be said about the number, sizes, or distribution patterns of the teeth. The coronoid(s) obviously possessed numerous teeth having the same characteristics as those of the dentary, but most notable is the presence of at least one dominant, tusk-like tooth whose tip fitted into the fenestra in the palatine when the jaws were tightly closed. A cross-sectional break of the skull with tightly closed lower jaws (CM 34100) clearly shows this structural relationship. None of the teeth of the skull or lower jaw exhibit any labyrinthine infolding or surface texture.

Postcranial skeleton.—The postcranial skeletal materials have for the most part suffered the same sorts of preservational imperfections seen in the skulls. The recalcitrant matrix and the extremely small and fragile nature of the bones have made extensive preparation impractical or nearly impossible. Moreover, because none of the specimens is complete, and in the few instances where a substantial part of the postcranial skeleton exists it is tightly compressed into discontinuous coils or loops, a systematic approach to expose specific regions of the postcranial skeleton was not possible. Much of what is described was exposed by weathering or by fracturing the fossil-containing nodules.

The number of presacral vertebrae cannot be determined, even though a considerable portion of the column is present in at least two specimens (CM 28581, and 41721). Incomplete atlases are present in series of seven cervical vertebrae in CM 28583 and 41723, and singly with the holotypic skull. In these instances it is mainly the centrum of the atlas that is preserved or is visible, and it conforms to the unique microsaurian structure of the atlantal centrum. The anterior articular surface is much broader transversally than corresponding surfaces of succeeding centra. It is divided into a wide, well-developed median “odontoid” process that fits into the recessed basioccipital, and laterally flanking surfaces that contacted the exoccipitals. The transverse width (5.0 mm) of the anterior end of the atlantal centrum of CM 41723 exceeds the length (3.4 mm) and width (about 2.5 mm) of the posterior end by 47% and 100%, respectively. The rib facets cannot be seen. Though a portion of the base of the right half of the atlantal neural arch is present in the holotype, it is too incomplete to be informative. The cervical and trunk vertebrae (Fig. 11) appear to be essentially identical. The centra are holospondylous, and their notochordal, amphicoelous structure gives them an hourglass-shaped internal passage. The lateral surfaces are moderately constricted just beneath the pedicel of the neural arch, whereas the ventral half of the centrum is broadly rounded in transverse section. There is a slight outward flaring of the ends of the centrum to form an expanded, circular rim surrounding the notochordal funnel. The posterior rim of the centrum is noticeably more developed than the anterior rim

to accommodate the capitular articulation of the rib associated with the succeeding vertebra. A distinct neurocentral suture is evident in all the specimens. The pedicels attach to the anterior two-thirds of the dorsal length of the centrum. Extending laterally from the anterior end of the pedicel is a small but distinct transverse process. The neural arches are low, and the zygapophyses do not appear to extend beyond the level of the lateral margins of the centrum. The anterior zygapophyses barely extend beyond the end of the centrum, whereas the posterior zygapophyses extend well beyond. The zygapophyseal planes are essentially horizontal. The very low and weakly developed neural spine is angled posteriorly, so the apex is positioned behind the pedicel. No sacral or caudal vertebrae have been recognized. Although ribs are ubiquitous, none are sufficiently preserved or exposed to warrant description.

The shoulder girdle is present in several specimens (CM 34902 and 41721), but is best exposed and preserved in CM 28583 (Fig. 12A, B), where all the elements except the cleithrum are represented. The cleithrum may be present on the incompletely prepared left side. The anterior plate of the T-shaped interclavicle of CM 28583 is modestly developed. It does not extend beyond the anterior margins of the ventral plates of the clavicles, with which it seems to be correctly articulated. The posterior stem appears to be very short, barely extending between the coracoid plates, but this may be due in part to poor preservation. The narrowly subrectangular ventral plates of the clavicles are widely separated at the midline. The lateral half of the ventral plate of the clavicle widens somewhat by a step-like expansion of its posterior margin. The approximately right angle union between the ventral plate and dorsal stem is abrupt, with the stem inclined posterodorsally. The dorsal half of the thin stem tapers to a point as it extends to the level of the dorsal margin of the scapula. A cleithrum has not been identified in any of the specimens. The scapulocoracoid is ossified as a single element, but can be divided arbitrarily into a vertical scapular blade and a horizontal coracoid plate that meet at a right angle. The scapular blade is broad anteroposteriorly but low, and its free margin is smoothly rounded. In CM 34902 the scapular blade appears to be relatively higher. In ventral view the essentially flat coracoid plate has a kidney-shaped outline, with the convex margin directed toward the midline. The coracoid extends for a considerable distance behind the deeply incised, U-shaped notch of the glenoid on the lateral margin, where it tapers to a blunt point. The outer portions of the fore and aft margins of the glenoid are continued on strongly developed, laterally projecting protuberances. A coracoid foramen lies a short distance anteromedially to the glenoid. In CM 28583 the coracoids are widely separated from along their medial borders and from the dermal elements of the girdle anteriorly. This is most probably due to incomplete ossification of the coracoid margins, but could also be simply the result of displacement. Lateral view of the scapulocoracoid reveals the glenoid as long and low, with the anterior and posterior ends being at the same level. Despite its length, the glenoid is positioned well posterior of the scapular blade. Adjacent to the posterior border of the glenoid the dorsal margin of the coracoid rises in a prominent triangular process for the attachment of the coracoid head of the triceps muscle. A supraglenoid foramen was not detectable.

The entire forelimb is represented only in CM 41721, where the nearly complete and articulated right humerus, radius, and ulna, are well exposed (Fig. 12C). A nearly complete but poorly preserved left humerus is articulated with the shoulder girdle of CM 28583, and the proximal end of the right humerus is preserved articulated with the scapulocoracoid of CM 34902. The lightly built humerus of CM 41721 is approximately 9.8 mm long. The proximal end is exposed in posterior view and is approximately 3.3 mm, whereas the distal end, exposed essentially in all but its anterior and distal views, is 4.0 mm wide. The expanded ends occupy planes set at right angles to one another and are joined by a short, narrow shaft, with a minimum diameter of about 1.0 mm. An entepicondylar foramen is evidently absent. Areas of muscle attachment are not clearly discernible, and the articular areas for the radius and ulna are hidden by these elements. The radius is 4.7 mm long, or slightly less than half the length of the humerus. The slightly expanded subcircular proximal end has a width of about 0.8 mm. The shaft of the radius is slender, having a minimum diameter of about 0.4 mm, but the distal end widens moderately mediolaterally to about 1.2 mm. The ulna, exposed mainly in posterior view, is 5.8 mm long or nearly 60% of the length of the humerus. The large olecranon is about 1.5 mm wide across its lateral face, and the fully ossified olecranon process extends well beyond the well-developed semilunar notch. From above the shaft narrows to a minimum diameter of about 0.4 mm, then expands somewhat shortly before the flat distal end to about 0.7 mm. A few carpal elements are preserved closely associated with the forelimb of CM 41721, but are too scattered and incomplete to warrant description.

The pelvic girdle is seen only in CM 28581, but preservation is so poor that an illustration would not add substantially to its description. The two halves of the puboischiadic plate are narrowly separated, missing mainly the ischium of the left, and are exposed in ventral aspect; only the right ilium is seen, and then only in vertical section is a result of a break in the block of matrix containing the specimen. The ilium and puboischiadic plate join to form an internal angle between them of about

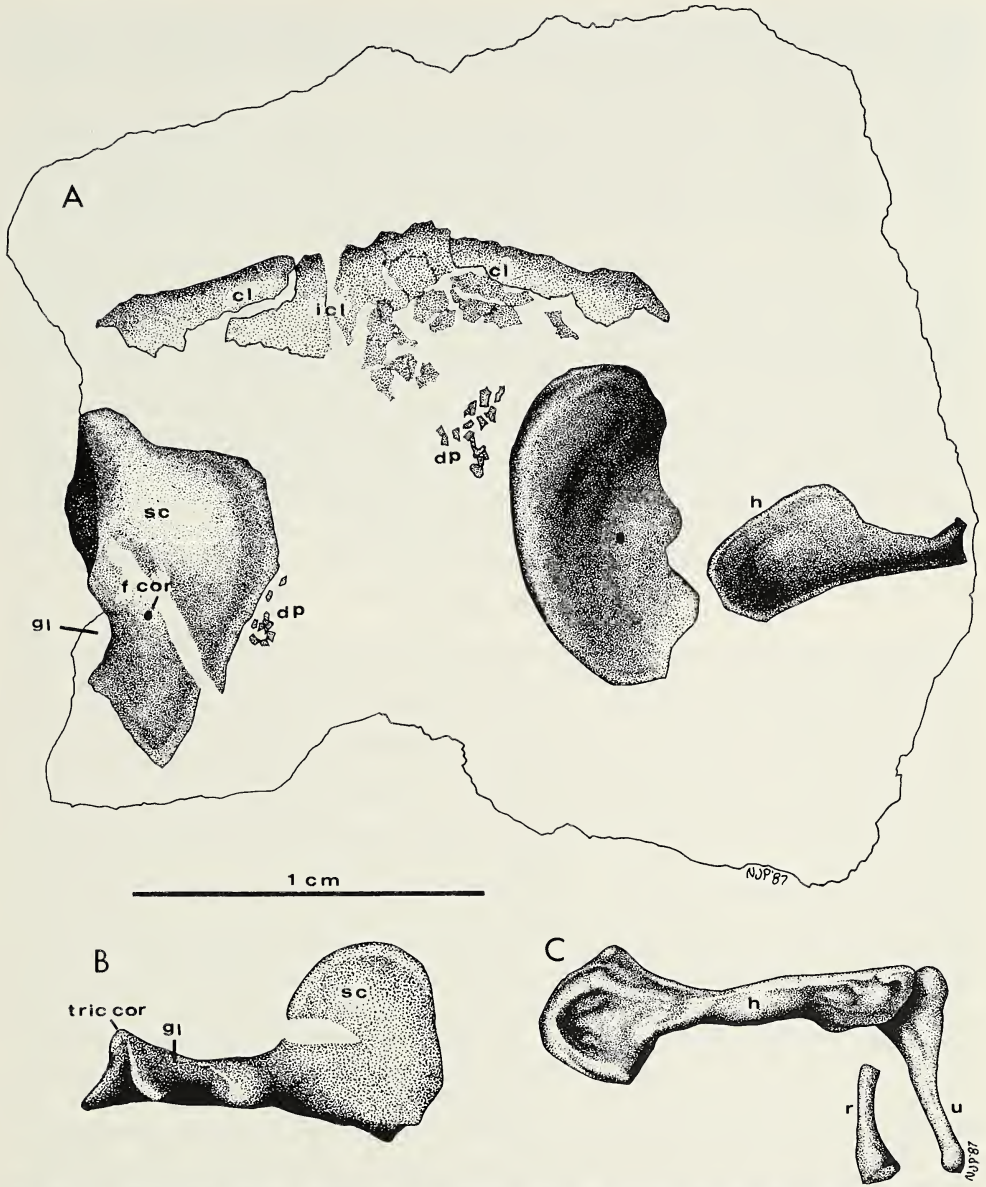


Fig. 12.—*Stegotretus agyrus*, paratypes. A, ventral view of pectoral girdle with left humerus and scattered polygonal dermal plates; and B, lateral view of right scapulocoracoid of CM 28583. C, posterior view of right forelimb of CM 41721.

135°. The dorsal shaft of the ilium is long, narrow, and divided distally into dorsal and posterior processes. The anteroposterior length of the puboischadic plate is about 12.5 mm. There is no clear suture separating the pubes and ischia, but it is safe to say that the external surface of the pubis is rather flat and quadrangular in outline. It has a prominent obturator foramen a short distance medial to the acetabulum. In ventral aspect the ischium has roughly the shape of a long, narrow, posteriorly pointing triangle. Its anterolateral corner is thickened to buttress strongly the posteroventral margin of the acetabulum. The anterior end of the free lateral margin of the ischium angles abruptly posteromedially for a short distance, then moderately in a slightly convex arc to the posterior end of the

element. The medial margin of the ischium is straight for most of its length posteriorly. It is not known, however, whether the ischia were joined along their entire length medially or for only some portion anteriorly, with the remaining posterior portion of the borders forming a narrow, posteriorly widening, V-shaped notch between them.

The femora are articulated with the pelvis of CM 28581 and the right tibia is also present. These are the only hindlimb elements that have been identified, and they are so badly preserved that their illustration is impractical. The right femur is nearly complete, but is only partly exposed as a result of breaks in the block of matrix containing the specimen. It is about 9.6 mm long. The head is terminal with a broadly convex dorsal surface, and ventrally there is a prominent internal trochanter that is set off from the head by an abrupt notch. Compared to a width of 4.0 mm for the broadly expanded distal end, the circular shaft narrows to a diameter of about 1.3 mm. The anterior and posterior condyles are well developed and separated dorsally by a well-defined intercondylar fossa. The right tibia, about 4.4 mm long, is exposed in anterior and medial views. The proximal end is greatly expanded, measuring about 2.4 mm in mediolateral width. A shallow, broad groove divides its anterior face into medial and lateral condylar-like ridges whose proximal articular surfaces correspond to those of the anterior and posterior condyles of the distal end of the femur. The subcircular shaft narrows to a least diameter of about 1.0 mm. The distal end of the tibia is slightly expanded, measuring about 1.5 and 2.0 mm in mediolateral and anteroposterior widths, respectively. The distal articular surface is beveled at about a 50° angle to the long axis of the bone. A small portion of the pes is closely associated with the right hindlimb of CM 28581, but it is too poorly preserved to be informative.

Small patches of polygonal dermal plates are found beneath the ventral portion of the shoulder girdle of CM 28583 (Fig. 12A), 34902, and 41721. They typically have a length of only a few tenths of a millimeter, but may reach about 0.6 mm in greatest diameter.

RELATIONSHIPS

The Microsauria have been exhaustively reviewed by Carroll and Gaskill (1978), and *Stegotretus agyrus* complies strictly with their definition of the order. Specifically, *S. agyrus* is assigned to the Microsauria on the basis of: 1) presence of only a single bone in the temporal series of the skull, identified as the tabular (the supratemporal and intertemporal being absent); 2) the absence of an otic notch or anything like an otic embayment; and 3) a cranio-cervical joint in which the basi-exoccipital complex forms a broad, "strap-shaped" socket for the "odontoid" structure of the typically single-unit atlas. Carroll and Gaskill (1978) recognized two suborders, Tuditanomorpha and Microbranchomorpha, distinguished mainly by skull roof differences and the number of digits in the manus. *S. agyrus* is clearly assignable to the Tuditanomorpha because the postfrontal and postorbital are subequal in size and broadly contact the tabular. Carroll and Gaskill (1978) recognized seven tuditanomorph families, containing 21 genera and ranging from the Lower Pennsylvanian to the Lower Permian in age. Their diagnoses are based almost entirely on phenetic similarities that combine, without distinguishing, derived and primitive characters. Using their family definitions, *S. agyrus* could be assigned to more than one of the tuditanomorph families. Although Carroll and Gaskill recognized two informal subgroups within the Tuditanomorpha (one comprising the families Hapsidopareiontidae, Tuditanidae, and Pantylidae and the other Gymnarthridae, Goniorynchidae, Ostodolepidae, and Trihecatontidae), they did not attempt to construct a phylogenetic scheme at either the familial or generic level. They cited an appallingly incomplete fossil record, wide variation in sizes, limb proportions, and dentitions, and the possibility that some of the characters have a functional base. All seven tuditanomorph families are believed to have descended from a common ancestor in the early Carboniferous, well before their first appearance in the Lower Pennsylvanian (Westphalian B), making it impossible to specify their interrelationships.

The question of the interrelationships of the tuditanomorph families was considered by Schultze and Foreman (1981). They were unable to assess the signif-

icance of the characters of a new tuditanomorph species, *Euryodus bonneri*, from the Lower Permian of Kansas, without a testable phylogenetic scheme. By utilizing Carroll and Gaskill's data and their "own judgment" (p. 8) they chose derived characters for constructing cladistic analyses of the tuditanomorph families (they excluded the poorly known Trihecatontidae) and of the species of the family Gymnarthridae to which they assigned *E. bonneri*. They validated the monophyletic integrity of the families and redefined the family Gymnarthridae. They also altered Carroll and Gaskill's classification by changing the familial assignments of four genera.

Langston and Olson (1986) agreed with Carroll and Gaskill's (1978) opinion that the great diversity of the known microsaurs indicates how poorly the group is represented, arguing that it is presently futile to attempt to recognize consistent suites of characters that will unite the genera into reasonably well-defined families. They cite the cladistic analyses presented by Schultze and Foreman (1981) as proof of their observation. It is pointed out that in both schemes plesiomorph characters predominate and autapomorphies occur in most of the lineages, but, most importantly, synapomorphies are few and very narrowly distributed. They contend (p. 13) that this "distribution of characters emphasizes the great variety of microsaurs stressed by Carroll and Gaskill (1978) and also, of course, renders many of them useless for taxonomic purposes, given the current state of knowledge."

Despite the fact that the family diagnoses are not based on derived characters, there are no serious problems determining the closest relatives of *Stegotretus agyrus*. The studies by both Carroll and Gaskill (1978) and Schultze and Foreman (1981) provide a basis for evaluating the relative advancement of characters. This is especially true of the latter study in which character states of tuditanomorphs were evaluated by comparison with the closest possible outgroup, the Microbrachomorpha, and the anthracosaur labyrinthodonts, considered the most primitive and most closely related sister-group outside of the microsaurs. The Microbrachomorpha were also judged the more primitive of the two microsaur suborders by Carroll and Gaskill (1978). In both studies Tuditanidae are considered the most plesiomorphic family of tuditanomorphs. Furthermore, in the phylogenetic scheme arrived at by Schultze and Foreman the families Pantylidae, Hapsidopareiodontidae, Gymnarthridae, Goniorhynchidae, and Ostodolepidae represent, respectively, successively more apomorphic groups. On the basis of shared-derived characters of the skull roof, palate, lower jaw, and postcranial skeleton, *S. agyrus* is most closely related to *Pantylus* of Pantylidae.

A feature of the skull roof unique to *Stegotretus* and *Pantylus* is the overlapping sutural pattern of the lacrimal-jugal contact beneath the orbit. In *Stegotretus* the lacrimal narrows posteriorly to a wedge-like process that extends above a similar anterior extension of the jugal. In *Pantylus* this contact differs only in having a more extensive overlap and much narrower processes. The primitive state of this character is undoubtedly the simple, narrow lacrimal-jugal contact found in most microsaurs, including the tuditanids, whereas a narrow separation between the two elements, as seen in some forms such as the gymnarthrid *Cardiocephalis* and the ostodolepid *Micraroter*, probably represents a second derived character-state. *Stegotretus* and *Pantylus* are unique in sharing the obviously derived character-state of a prominent dorsal expansion of the maxilla, though it is more developed in *Pantylus*. The presence of a noticeable ventral expansion of the postorbital cheek region further separates *Stegotretus* and *Pantylus* from all other microsaurs.

In both genera, though greatly exaggerated in *Pantylus*, the expansion is formed mainly by the jugal which conceals the posterior end of the upper tooth row from lateral view.

Stegotretus and *Pantylus* exhibit two unique, shared-derived characters of the palate: the internal naris is greatly enlarged and obviously accommodated the first and second dentary teeth; and the second dentary tooth is enormously enlarged over the others of the dentary series. Both these features are more developed in *Pantylus*, where a greater expansion of its internal naris has resulted in a much more reduced vomer. The unusual absence of an ectopterygoid in *Stegotretus* is known elsewhere only in *Pantylus* and is clearly a derived character. It must be admitted, however, that the palate of many microsaur is poorly known, and this character could be easily misinterpreted in them. There is also some reason to believe that in some lines a tendency may have existed toward reduction of the ectopterygoid. For example, the ectopterygoid is reduced considerably in *Hapsidopareion*, and in the microbrachomorphs *Odonterpeton* and *Hyloplesion*, where a corresponding enlargement of the palatine of *Hyloplesion* also occurs.

Only *Stegotretus* and *Pantylus* exhibit the unique character of a single, conspicuously large, tusk-like coronoid tooth. The manner in which this tusk-like tooth is accommodated when the jaw is closed, however, is expressed as different derived character-states in the two forms. In *Pantylus* the tip of the crown fits into a small toothless area located near the center of the palatine and immediately behind a very large, dominant tusk-like tooth, whereas in approximately the same area on the palate of *Stegotretus* a large circular fenestra accommodated the crown of the coronoid tooth.

The scapulocoracoids of *Stegotretus* and *Pantylus* are remarkably similar and in several shared-derived features are distinct from those of other microsaur. In both forms the essentially flat coracoid and scapular portions meet in an abrupt angle of approximately 90°. The coracoid extends well posterior to the scapular blade, and the glenoid is positioned well posterior to the scapular blade. Also unique to *Stegotretus* and *Pantylus* is the long, narrow glenoid, whose anterior and posterior extremities are at the same level. A well-developed triangular process adjacent to the posterior border of the glenoid for the coracoid head of the triceps muscle is also unique to these genera.

In addition to the derived characters shared only by *Stegotretus* and *Pantylus*, there are other characters that are also shared with a few other microsaur. One such character is the reduction of the marginal dentition. Six, possibly seven, premaxillary teeth is the primitive number, as seen in tuditanids, and the otherwise lowest count of three occurs in *Pantylus* and *Euryodus primus*. The lowest and most derived state of two premaxillary teeth occurs in *Stegotretus*. Similarly, the low number of 11 or 12 maxillary teeth in *Stegotretus* is a derived state relative to the approximately 16 to 26 recorded in all other microsaur (the highest being in Tuditanidae) except for nine in *Pantylus* and ten in the gymnarthrids *Cardiocephalus* and *E. primus*. As would be expected, there is a corresponding reduction in the number of dentary teeth in these forms. The highest numbers of dentary teeth (26–28) occur in the tuditanids and the lowest in *Pantylus* (9), the gymnarthrids *Cardiocephalus* (10, 11) and *Euryodus* (11, 12), and *Stegotretus* (10–12), whereas the remaining tuditanomorph families exhibit an intermediate state (16–23). Among the microsaur only *Stegotretus*, *Pantylus*, *Trachystegos megalodon* (a questionable pantylid, see below), and gymnarthrids exhibit noticeable heterodonty of the upper marginal teeth. *Stegotretus*, *Pantylus*, and *E. primus* are the

only microsaurs in which the first premaxillary tooth is dramatically enlarged over the second and third. In *Pantylus* and *E. primus* the first premaxillary tooth is the largest of the upper jaw series except for a maxillary "canine," whereas in *Stegotretus* it may be subequal to the largest maxillary tooth. In *Stegotretus* the largest maxillary teeth are located near the middle or toward the anterior end of the series. This most closely resembles the condition in gymnarthrids and the poorly known *Trachystegos megalodon* (Carroll, 1966) in which the largest teeth are typically positioned near the middle of the series. Maxillary heterodonty in *Pantylus* is quite distinct from that of all other microsaurs in that the first maxillary tooth is approximately twice the size of the next largest and immediately succeeding teeth. *Stegotretus*, *Pantylus*, *Trachystegos*, and gymnarthrids are united by the shared-derived character of large, stout, bluntly pointed marginal teeth. Finally, the high skull width to skull length ratios of about 0.96 in *Stegotretus* and 1.04 in *Pantylus* most likely represent a derived state. Similar values of about 0.94 or 0.95 are seen only in the tuditanid *Crinodon* and the ostodolepid *Micraroter*, whereas values for all other tuditanomorphs range from about 0.65 to 0.83 (Carroll and Gaskill, 1978).

There is another possible derived character that *Stegotretus* and *Pantylus* have in common with just one other microsauro. The patches of small polygonal dermal plates seen on the ventral side of the shoulder girdle in *Stegotretus* and *Pantylus* have been noted elsewhere only in the hapsidopareiodontid *Saxonerpeton* (Carroll and Gaskill, 1978).

The sister-group relationship between *Stegotretus* and *Pantylus* is challenged by a single derived character. The ventralward expansion of the jugal in the postorbital cheek region in *Stegotretus* conceals an unusual derived character-state, the narrow contact between the maxilla and quadratojugal. Though *E. primus* is the only other microsauro to exhibit this feature, the contact between maxilla and quadratojugal is not hidden from lateral view by the jugal, and the quadratojugal ends posteriorly far short of the occipital surface, as is typical of the gymnarthrids.

In summary, *Stegotretus* and *Pantylus* are linked by at least 10 derived character-states shared by no other microsauro. A few derived character-states present in *Stegotretus* and *Pantylus* are also present in some other microsaurs. Though they do not necessarily support a relationship between *Stegotretus* and *Pantylus*, they are consistent with it. Only one derived character-state is shared by *Stegotretus* and a microsauro other than *Pantylus*. Thus, a sister-group relationship between *Stegotretus* and *Pantylus* seems well founded.

Stegotretus and *Pantylus* differ in a number of derived character-states, some autapomorphic. In addition to the characters discussed above, *Pantylus* is clearly derived relative to *Stegotretus* in the following prominent characters: 1) absence of a parietal opening; 2) otic elements join with the parasphenoid to extend far laterally as they form the large, ventrally facing fenestra ovalis; 3) dorsal blade of ilium not divided into dorsal and posterior processes; 4) clavicles suturally jointed at midline; 5) significantly larger skull, and 6) pubis nearly, if not completely, excluded from acetabulum. But *Stegotretus* is clearly derived relative to *Pantylus* in possessing a maxilla-quadratojugal contact, the palatine having a large circular fenestra, the reduction of the number of premaxillary teeth to two, and the loss of the entepicondylar foramen of the humerus. Thus, on balance, it seems clear that *Pantylus* is much more specialized than *Stegotretus*. Nevertheless, derived features of *Stegotretus* exclude it as a direct ancestor of *Pantylus*.

In Carroll's (1966) original description, the poorly known Lower Pennsylvanian *Trachystegos megalodon* is viewed as a possible distant antecedent to *Pantylus*, and both genera are depicted as the sole members of a distinctive gymnarthrid lineage. *T. megalodon* was again viewed as a possible predecessor to *Pantylus* by Carroll and Gaskill (1978), but because they also judged *Pantylus* distinct enough to warrant separate family status, both genera were included in Pantylidae Case (1911). The family diagnosis by Carroll and Gaskill (1978) is based, however, entirely on the type genus, and *Trachystegos* and *Pantylus* do not exhibit any derived features which could safely be considered unique to them. Carroll and Gaskill (1978) noted that, as in *Pantylus*, (but to a far lesser degree) the skull of *Trachystegos* is large and conspicuously sculptured, and the teeth are massive. As also noted by Schultze and Foreman (1981), size is a very weak character for basing relationships. However, the skull of *Pantylus* is significantly larger than that of any other microsauro, and in this feature *Pantylus* is undoubtedly derived. Further, it is ambiguous whether the sculpturing is a derived or primitive character, and massive teeth are also present in gymnarthrids. Similarity between humeri attributed to *Trachystegos* and those of *Pantylus* is also cited by Carroll and Gaskill as a reason for assigning *Trachystegos* to Pantylidae, yet they also noted that the humerus of *Trachystegos* resembles that of the primitive tuditanid *Asaphostera*. Schultze and Foreman (1981) considered the assignment of *Trachystegos* to Pantylidae incorrect, because it does not conform to the characters of the family. Thus, as concluded by Schultze and Foreman, the relationships of *T. megalodon* are at present indeterminate, and its family status is probably best relegated to *incertae sedis*. If *Trachystegos* is removed from Pantylidae, then the several recognized synapomorphies linking *Stegotretus* and *Pantylus* can also serve to firmly define the family Pantylidae (see SYSTEMATIC PALEONTOLOGY section above).

ECOLOGY

Parallels in the mode of preservation of the *Stegotretus agyrus* specimens with that of the presumed aestivating phase of the elongate Permo-Pennsylvanian amphibian *Lysorophus* suggest that the former may have been preserved in a similar aestivating condition. *Lysorophus* specimens preserved in an aestivating, rather than free-swimming, phase characteristically occur tightly coiled in predominantly dolomitic, ovoid nodules and in locally high concentrations distributed over only a few square meters (Olson, 1956, 1971; Olson and Bolles, 1975). Olson and Bolles (1975) note the absence of a distinct boundary between the nodules and surrounding matrix, and that the more resistant nodules weather free from the enclosing sediment. Of the 21 *S. agyrus* specimens that include skulls, at least two are articulated with the greater part of the postcranial skeleton tightly coiled in what may have been an aestivation position. Breaks in the coils and displacement of parts of the skeleton are very likely the result of postmortem distortion. Many other specimens include skulls with large portions of the postcranial skeleton, and it is very probable that all the individuals were originally complete. There is no evidence of hydraulic transport of the specimens, and their incompleteness is attributed to erosion and weathering, rather than primary depositional processes. Despite the fact that the caliche nodules and calcite-rich siltstone pebbles containing the specimens were preserved as a surface-lag deposit, they were found distributed over an area of only a few square meters. Strong sedimentological evidence presented here and elsewhere (Berman et al., 1985,

1987; Eberth, 1987) indicates that the Cutler Formation of north-central New Mexico was deposited in a semi-arid climate marked by short wet seasons. That the specimens may represent an aestivation assemblage is consistent with this paleoclimatic interpretation.

POSSIBLE PANTYLID MICROSAUR

In addition to the microsauro described above, only one other possible microsauro specimen has been reported from New Mexico. In listing the vertebrates that have been collected from the Anderson quarry in the Cutler Formation near Arroyo del Agua, Langston (1953, p. 360) refers to "a mandible [UCMP 39178] of a form near *Pantylus*" without further comment. The Anderson quarry (see Langston, 1953, for description of locality) is located about 1.3 km southwest of the type locality of *Stegotretus agyrus* in SE1/4NW1/4SW1/4, Sec. 8, T 22 N, R 3 E. The Anderson quarry is approximately 70 m stratigraphically above the base of the classic collecting beds of the Arroyo del Agua area, including the type locality of *Stegotretus*. This horizon is certainly Early Permian Wolfcampian in age (Fig. 2).

The lower jaw consists of the joined anterior portions of both rami (Fig. 13). In most instances the sutures are difficult to trace, but it is believed that the dentaries, angulars, splenials, and prearticulars are represented, at least in part. The rami of the mandible meet in a very wide angle, suggesting that the skull was very broad. The rami are subrectangular in cross-section, being much wider than high, particularly a short distance anterior to the adductor fossa, where the measurements are a little over 10 mm and about 6 mm, respectively. Despite having suffered a considerable amount of weathering, the ventral and lateral surfaces of the jaw exhibit a sculpturing pattern of deep pits surrounded by low ridges. All that remains of the teeth are very low bases.

The dentary is the dominant element of the jaw and is completely fused with its mate at the symphysis without any sign of a suture. There is, however, a very slight, narrow swelling along the midline of the ventral surface of the fused dentaries that may represent the position of the original symphyseal suture. There is a major break in the left dentary near this ridge. Ventrally the dentary is exposed as a large, flat plate that nearly reaches the medial margin of the jaw. Here it contacts the splenial in a straight suture that parallels the medial margin of the jaw. The dentary extends posteriorly to what was probably about the midlength of the jaw, contacting what is presumed to be the angular in a nearly straight suture that is oriented slightly anteromedially with respect to the long axis of the ramus. In ventral view the right dentary appears to have a greater posterior extent than the left. The lateral exposure of the dentary is far more extensive, extending the full preserved length of the more complete right ramus. At a level a short distance posterior to the last marginal tooth and lateral to the adductor fossa of the right ramus, there is an abrupt narrowing of the dentary by a step-like constriction of its lateral surface. The dorsal exposure of the dentary is rather narrow except for a pronounced widening in the symphyseal region.

The tooth bases of the dentaries and coronoids clearly indicate a powerful dentition of very stout teeth, none of which show any signs of labyrinthine infolding. The bases of nine teeth, including a symphyseal tooth, can be discerned on the right dentary, and the wide space between the sixth and the next succeeding tooth base was obviously occupied by an additional tooth that was completely destroyed by weathering; the left dentary contains only the first six postsymphyseal tooth bases. Judging from basal diameters, the first postsymphyseal tooth of each

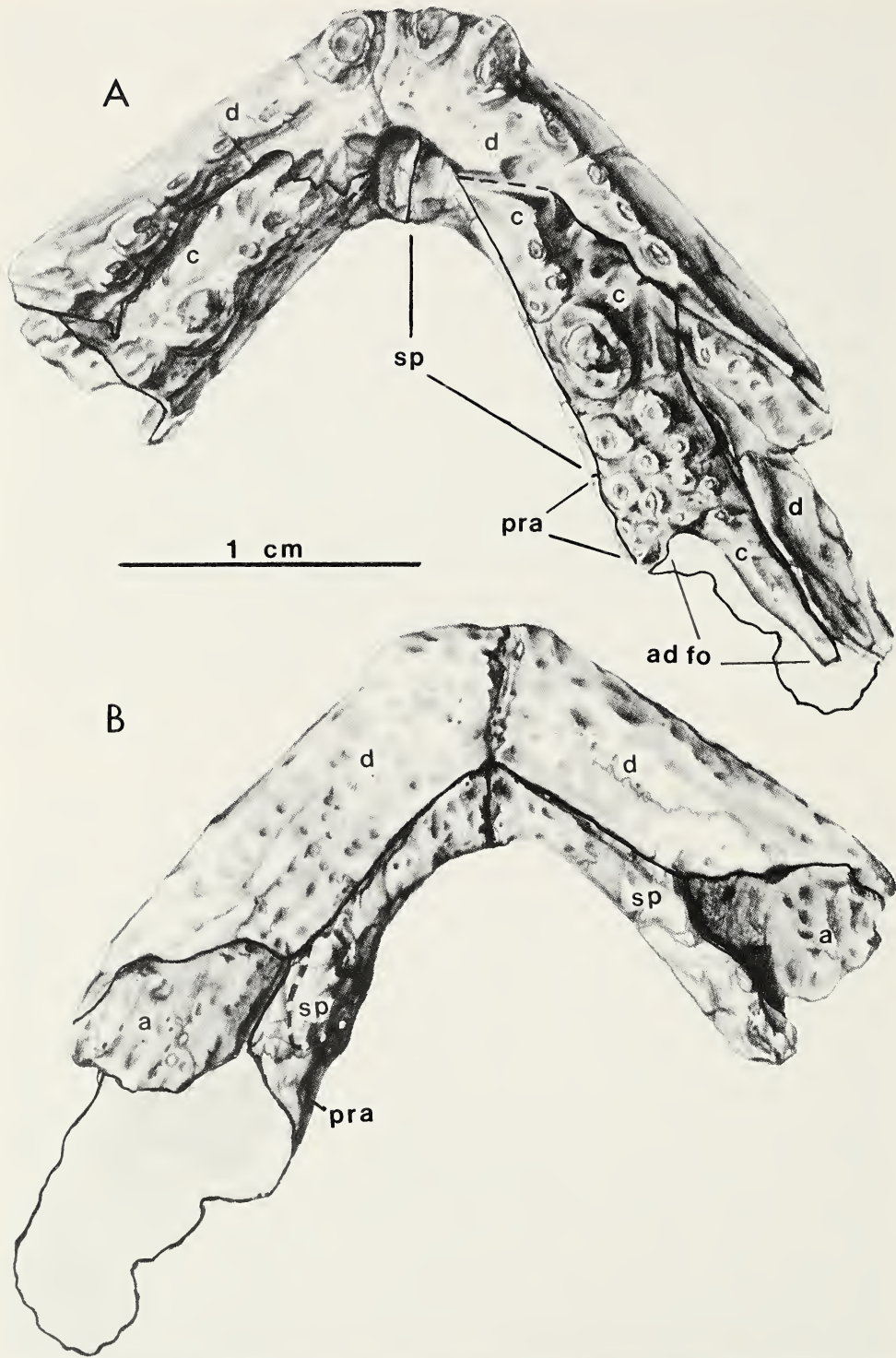


Fig. 13.—A, dorsal; and B, ventral views of possible pantylid microsauroid mandible UCMP 39178.

ramus was enormously enlarged over all the others of the series. The base is somewhat oval anteroposteriorly, with a greatest diameter of about 3.7 mm for that of the right ramus. The subcircular symphyseal tooth, though also very large, has a considerably smaller diameter of about 2.3 mm. The second through sixth postsymphyseal teeth of the right ramus are relatively very small, subequal in size, rather widely spaced, and distinctly oval in basal outline with the long axis parallel to that of the jaw ramus. The last three teeth of the right dentary are slightly smaller, more closely spaced, and are circular in basal section. The last three teeth are also aligned in a slightly more anteromedially directed row than the rest of the teeth.

Only a single splenial can be recognized in each ramus. Seen ventrally it forms a narrow strip along the medial margin of the jaw. The splenials join in a symphyseal suture. Here they expand noticeably in width, forming the ventral floor of a large, deep, smooth pocket that penetrates the posterior surface of the fused dentaries. The floor of the pocket is divided by a low, narrow ridge along the symphyseal suture. The splenial wraps around the ventromedial edge of the jaw to form a smooth, flat, thin, sheath-like covering of the entire vertical inner surface of the jaw from the symphysis to a level a short distance anterior to the adductor fossa. Only the right ramus is well enough preserved to allow a tentative determination of the posterior contact of the splenial with the prearticular. Ventrally this contact appears to be chevron-shaped; it then extends vertically across the entire width of the inner surface of the jaw.

The right coronoid appears to be essentially complete and is exposed on the dorsal surface of the jaw mainly as a broad tooth-bearing plate. The coronoid is confined laterally by the dentary, whereas medially it is bounded for most of its anterior length by the sheath-like covering of the splenial and for a short distance posteriorly by the prearticular. Posteriorly the coronoid forms the anterior and the anterolateral margin of the adductor fossa. Along the anterolateral margin it rises posteriorly into a very low coronoid process, then descends to its anterior height. The coronoid contains the bases of 17 large teeth of greatly varying sizes. They are clustered with moderate spacing into a narrow, triangular area that widens posteriorly as it extends from nearly the anterior end of the coronoid to the anterior margin of the adductor fossa. The teeth of the anterior half of the tooth battery are confined to the medial side of the dorsal surface of the coronoid. The toothless lateral portion of the dorsal surface of the coronoid slopes steeply ventrolaterally and meets the dentary well below the level of its dorsal surface, forming a deep, trough-like depression along their contact. Near the anterior end of the tooth battery is a single, extremely large, oval tooth base whose greatest diameter of about 4.2 mm is aligned with the long axis of the ramus. This is about 13% larger than the large first postsymphyseal tooth of the dentary.

Only small portions of the anterior ends of the angular and prearticular are represented, and their relationships with neighboring elements appear to be typical for microsaurs.

DISCUSSION

The lower jaw UCMP 39178 cannot be assigned to the Microsauria on the basis of shared-derived characters. However, it does share with *Pantylus* and *Stegotretus* a number of characters, some unique to both genera among the microsaurs. This suggests assignment to Pantylidae and therefore indirectly to the Microsauria. As already noted, Langston (1953) recognized the closeness in form of UCMP 39178 to *Pantylus*, but without noting any specific similarities.

Similarities between UCMP 39178 and Pantylidae, as defined here, are most obvious in the dentitions, where they share two derived characters not seen in other microsaurids. *Stegotretus* and *Pantylus* are uniquely united by the enormous enlargement of the second dentary tooth. This character can also be recognized in UCMP 39178 if its symphyseal tooth is counted as the first tooth of the dentary series. Secondly, the presence of a single, dominant tooth on the coronoid in UCMP 39178 is a feature seen elsewhere among microsaurids only in *Pantylus* and *Stegotretus*.

The reduced number of dentary teeth in UCMP 39178 is matched most closely among the microsaurids by the pantylids *Pantylus* and *Stegotretus* with 9 and 10–12 teeth, respectively, and among the gymnarthrids by *Cardiocephalus* and *Euryodus* with 10 or 11 and 10 or 12 teeth, respectively. The posterior width of the skull of UCMP 39178, judging from the angle in which the rami of the mandible join, was obviously much greater than its length. Among the tuditanomorph microsaurids a high skull width to length ratio is not only characteristic of the pantylids, with *Pantylus* and *Stegotretus* having values of 1.04 and 0.96, respectively, but can also be calculated from the measurements given by Carroll and Gaskill (1978) for the tuditanid *Crinodon* and the ostodolepid *Micraroter*, with values of 0.95 and 0.94, respectively. The corresponding value for UCMP 39178 was likely greater than that of *Pantylus*.

The unusual step-like indentation of the lateral surface of the posterior half of the dentary of UCMP 39178 may indicate that, as in *Stegotretus* and *Pantylus*, the ventral margin of the postorbital cheek of the skull was greatly expanded and extended well below the level of the upper jaw margin. In *Pantylus*, where the ventral flange of the postorbital cheek is particularly exaggerated, Romer (1969: 22) notes a longitudinal shallow shelf in the region lateral to the adductor fossa of the lower jaw that corresponds to the lower boundary of the flange. This suggests that the lateral indentation of the posterior half of the dentary of UCMP 39178 may have accommodated a pronounced postorbital cheek flange as in *Pantylus*.

UCMP 39178 shows no strong likeness to any other Paleozoic taxon known to us, and we therefore recommend tentative assignment to Pantylidae.

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